Spring 2018

FACTORS INFLUENCING THE DISTIBUTION OF EGG-BEARING AMERICAN LOBSTERS (HOMARUS AMERICANUS)

Joshua Carloni
University of New Hampshire, Durham

FACTORS INFLUENCING THE DISTIBUTION OF EGG-BEARING AMERICAN LOBSTERS (*HOMARUS AMERICANUS*)

BY

JOSHUA THOMAS CARLONI

B.S., Johnson State College, 2002

THESIS

Submitted to the University of New Hampshire

In Partial Fulfillment of

The Requirements for the Degree of

Master of Science

In

Zoology

May, 2018

This thesis has been examined and approved in partial fulfillment of the requirement for the degree of Master of Science in Zoology

Thesis Director, Dr. Winsor H. Watson III
Professor of Zoology

Dr. W. Hunting Howell, Professor of Zoology

Dr. Jason S. Goldstein, Research Director, Wells National Estuarine Research Reserve

On 4/3/2018

Original approval signatures are on file with the University of New Hampshire Graduate School

ACKNOWLEDGMENTS

I would like to first acknowledge my family, for without them none of this would be possible. My Dad: Who taught me one of the most important lessons of my life-"anything is possible, if you put your mind to it." My mom, who encouraged me to follow my passion and always displayed a positive attitude regardless of the day. My brothers Travis and Justin: Building tree forts, dams and exploring the woods behind the old homestead really helped shape my curiosity which certainly helped with this research, glad we still get the chance to do some of that stuff together as adults. Last but certainly not least, I would like to thank my wife, who's a wonderful woman and words just can't do her justice. She has supported me at every step along the way. Thank you Jessica, I love you and look forward to the next chapter.

My lobster colleagues: I would first like to thank Carl Wilson, because, without his continual encouragement, I would have never pursued this degree. Jason Goldstein, whose approach to research has set a fine example, thanks for being a friend as well as a committee member. Hunt, I've always enjoyed our interactions, it usually involved conversations down near the water: a place where I think we're both most content. Clare McBane, who left this world much too soon, thank you for teaching me the importance of data collection. Doug Grout, thanks for all of your support, I appreciate your vision, you've been a great Chief. Next, my lobstermen friends, Vinnie Marconi, Joe Golter and Damon Frampton, without your knowledge none of this research would have been realized (really), thank you, you guys are great and you taught me that nature can be enjoyed in many ways. My last lobster acknowledgement goes to

Bob Glenn, whose approach to this profession has always resonated with me; common sense goes a long way in this field.

Finally, thanks to the guy who made this all come to fruition, Win Watson, I've learned so much from you, thanks for keeping up the old school approach to things, it's so important that you keep those youngsters working hard. You gave me this opportunity and your devotion to helping students succeed and realize their full potential over the past several decades is so damn impressive. Congrats on a wonderful career, you will be missed and enjoy the next chapter of your life.

I would also like to thank everyone else that was involved in my research: Conor O'Donnell for helping me with trap based research, much appreciated. Nate Rennels, thanks for putting up with some of my crazy ideas in the lab, you make all of this work. Catherine Callahan, thank you for helping with GIS work. Kara Villone, keep up the hard work, it will pay off some day. Additional thanks to Calvin Diessner, Ed Motyka, Meghan Owings and Rebecca Kibler. If I missed anyone I am sorry, thanks to all, this has been a lot of hard work, but one of the best experiences of my life.

Funding for this research was provided by The Wildlife Heritage Foundation, the University of New Hampshire Marine Biology Grant as well as equipment loans from Well Research Reserve, Maine Department of Marine Resources and Massachusetts Division of Marine Fisheries. Finally, thanks to UNH CCOM for use of their multi-beam data.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

FIGURE PAGE

ABSTRACT

FACTORS INFLUENCING THE DISTIBUTION OF EGG-BEARING AMERICAN LOBSTERS (*HOMARUS AMERICANUS*)

By

Joshua Thomas Carloni

University of New Hampshire, May, 2018

The overall goal of this research was to explore the factors that influence the distribution of egg-bearing (berried, ovigerous, eggers) lobsters along the coast of New Hampshire (NH), specifically near the Isles of Shoals (IOS). Initially, I determined the distribution of egg-bearing lobsters based on catch rates (#/trap haul) from New Hampshire Fish and Game Department's (NHF&G) Lobster Sea Sampling Program. Based on these data there appeared to be a higher abundance of these lobsters on the eastern side of the IOS, which is closer to areas that are deeper and characterized by higher current flow. To confirm this finding I designed a trap-based study to assess lobster population demographics on both sides of the IOS (east vs. west) (Chapter 1). Trawls (traps tied to a common line) were set on similar substrates, depths, and comparable soak times on both the east and west side of the IOS so non-biased comparisons could be made between the two areas. Results suggest that traps fished on the eastern side of the IOS caught a significantly higher number of egg-bearing lobsters than those set on the western side. There was also a higher abundance of eggers with pre-hatch eggs in shallow water, and more females in the process of hatching eggs in deep water. A similar pattern was also apparent in two other surveys conducted along the coast of NH; the Lobster Sea Sampling Program and the Coastwide

Ventless Trap Survey. These data, taken together, led to my hypothesis that egg-bearing lobsters move from shallow to deep water just prior to the time when their eggs are due to hatch.

In the summers of 2016 and 2017 I tested this hypothesis by tracking the movements of 12 late-stage egg-bearing lobsters using acoustic telemetry (Chapter 2). I acquired acoustic tags for these animals (VEMCO V13AP) that transmitted depth (m) and activity (m/s^{-2}) every ~ 90 seconds and logged these data using an array of fixed VR2W receivers in the same area where the trap survey was conducted. All but one (92%) of these lobsters moved to deep water prior to the time when we predicted their eggs would hatch, based on using the Perkins Eye Index assay from samples removed from pre-tagged animals just before they were released. A total of 3 lobsters (25%) hatched eggs in deep water (30-40 m) within the array, while 67% left the array generally in a south, southwesterly, direction towards deeper waters. These results supported my hypothesis and indicated that the behavior of berried females appears to shift just prior to the time when their eggs are predicted to hatch. At the end of both Chapters of this thesis I speculate on the advantages of this behavior and the factors that might guide the movements of these lobsters.

INTRODUCTION

American lobster (*Homarus americanus*) is harvested throughout its current geographic range in the northwest Atlantic Ocean, from North Carolina (United States) to Newfoundland and Labrador (Canada), and from inshore coastal waters to offshore depths of more than 2,000 feet. The commercial harvest of lobster in the United States is currently the most valuable single-species fisheries in the country (NOAA 2017). In the United States American lobster is managed by the Atlantic States Marine Fisheries Commission in cooperation with both state and federal partners. Currently the Gulf of Maine/Georges Bank (GOM/GBK) stock is at a time series high level of abundance, whereas, the Southern New England stock is considered depleted.

If a resource of this geographical size and magnitude is to be managed as a sustainable fishery, then it is imperative that regional populations are closely monitored and that we have a good understanding of the distribution, mating characteristics and habitat use of ovigerous female lobsters. Protection of egg-bearing females is at the foundation of the lobster management pyramid (ASMFC 2006; ASMFC 2009), and as climate change continues to affect the Gulf of Maine ecosystem; gaining a better understanding of how it might impact this segment of the population is paramount. Much of what we know regarding the distribution of this population-segment is based upon state/federal fisheries-dependent and fisheries-independent monitoring programs (ASMFC 2010; Glenn et al. 2011). While this provides researchers with information about their spatial and temporal distribution patterns, we still know very little about the biotic and abiotic factors that guide their movements.

In Southern New England (SNE), recent studies have shown that egg-bearing females are not residing in the same areas as previously documented when their eggs hatch, and scientists have speculated that this is the result of increasing ocean temperatures (ASMFC 2010; Glenn et al. 2011). Importantly, it has also been shown that larvae released in these new locations may be advected into areas that are unsuitable for survival (Glenn et al. 2011). There are clear signs that suggest similar scenarios may be imminent in the Gulf of Maine (GOM). Data collected in 2012 indicate it is the most intense warming event in the last 30 years (Mills 2013). Since 1982 temperatures in GOM have increased by an average of $0.026^{O}C$ per year, and since 2004 that rate has increased to $0.26^{O}C$ per year. So, the question remains, once temperatures increase in historic brooding grounds in the Gulf of Maine, will the distribution of egg-bearing females change?

To attempt to answer this question we first need to identify the areas currently being utilized by brooding females and try to understand why they prefer these areas. What physical and biological characteristics do these areas possess that make them attractive to ovigerous lobsters? It is well known that lobster movement is highly influenced by water temperature and it appears that in some regions females migrate offshore in the winter and inshore in the spring to increase the number of degree days for gonad development and to synchronize their molt/reproductive cycles (Aiken and Waddy 1986, Campbell and Stasko 1986, Waddy and Aiken 1995, Crossin et al. 1998, Goldstein and Watson 2015). This paradigm is well ingrained in modern-day lobster biology, and although it appears that temperature plays an important role in lobster movements, one cannot discount other factors, such as habitat, depth, light intensity and current speed/direction. Given the well documented cases of decapod crustaceans displaying directed movement to release larvae in favorable areas for optimal larval development and dispersal (Epifanio et al. 1984; Epifanio et al. 1988; Tankersley 1998, Goldstein 2012), it's reasonable to assume that factors other than temperature may play a role in the distribution of ovigerous American lobsters during periods of both egg brooding and hatching.

Habitat Use

The habitat use by different life history stages of American lobsters has been studied in detail. Early benthic phase lobsters (EBP, <40mm) appear to seek out complex habitat such as cobble (Wahle and Steneck, 1991). Furthermore, it has been shown that areas facing southwest have higher densities of newly settled lobsters. This pattern has been attributed to the southwest winds that are typical in the late summer/early fall on the coast of Maine (Wahle and Incze, 1997). It's clear that complex habitat provides protection for small, cryptic, early life stages of American lobster. In contrast, the habitat preferences of adult lobsters appear to be more flexible.

Dunnington et al. (2005) used seabed mapping and mark recapture methods to assess population densities on various habitats. Legal sized lobsters were equally dense in cobble, ledge and sediment habitats, as determined both with trap catches and dive surveys. The manuscript however, didn't present data with regards to egg-bearing females. Geraldi et al. (2009) used the same dataset as the aforementioned study and found that catchability of total lobsters was consistently higher on sediment as compared to hard substrate (i.e. cobble, boulder & ledge). Although more lobsters were captured in areas dominated by sediment, it does not mean those lobsters preferred sediment. They may have been moving through these areas during daily foraging excursions or short migrations. This study also did not present data relating to egg-bearing females in the results.

Lobster Movements

American lobster movements have been studied since to 1898, when Herman Bumpus released approximately 500 mature females near Woods Hole, Massachusetts (Krouse, 1980 review). This tagging study, as well as others that followed through 1950 showed that lobster movements were generally limited to <18km. It was not until 1957-59 when Robert Dow tagged 162 non-legal lobsters (i.e. sublegals, ovigerous, v-notch and oversize) in waters along the coast of Maine that it was discovered that some lobsters make extensive movements (Dow, 1974). For example, one lobster in Dow's study traveled 138 miles in 7 months. To date there have been well over 40 studies conducted with some form of active or passive tagging device and there are certain patterns that tend to hold true for lobster movements throughout the range, as well as some discrepancies.

It's well established that smaller lobsters, in particular EBP lobsters, are cryptic and move little from areas which provide shelter from predators (Wahle and Steneck, 1992), and movement increases at larger sizes (Morrissey, 1971; Dow, 1974; Krouse, 1980 Review; Campbell and Stasko, 1985; Campbell and Stasko, 1986, Campbell, 1989). Several studies have shown that adult lobsters tend to exhibit seasonal movement patterns, migrating to deeper water in the colder months and to shoal waters in the warmer months (Cooper and Uzmann, 1971; Campbell and Stasko, 1986; Campbell et al., 1984; Krouse 1980 review; Campbell and Stasko, 1986; Campbell 1986). Authors of these papers have hypothesized that these directed movements increase the rate of egg development, by increasing the degree days they accumulate. Finally, it is generally accepted that water temperature has a strong influence on these movements. It has been demonstrated they will behaviorally thermoregulate (Crossin et al., 1998) and can detect very small changes in temperature (Jury and Watson, 2000).

Research has also been conducted on the movements of egg-bearing females, but to a much lesser extent. In 1965, 1,258 egg-bearing females were taken from offshore waters and relocated in Narragansett bay (Saila and Flowers, 1968). In general, females tended to stay in shoal water until their eggs hatched and then they tended to move back towards the area of original capture. Another study conducted in 1969-1970 on the eastern shore of Cape Cod, concluded that ovigerous females with ripe eggs moved the greatest mean distance of all groups tagged (Estrella and Morrissey, 1997). Conversely, lobsters tracked in NH via telemetry showed that females without eggs moved shorter distances than mature females without eggs (Watson et al., 1999). Campbell (1986) tagged 2,139 ovigerous females near Grand Manan and found that of the total 1,877 recaptures, 75% moved <15 km. However, some exhibited shallow to deep water migrations of > 20 km, with recaptures in shallow water (<20 m) in the summer-fall and deep water (>200 m) in the winter-spring. The author concluded that migrations were undertaken in order to maximize degree days for egg development and that warmer shallow waters may provide a survival advantage for larval stage lobsters.

A cooperative study conducted by Steneck (2000) and commercial fishermen along the coast of Maine in 1998 and 1999 reached the same conclusions as Campbell. Approximately 1,500 broodstock lobsters (v-notched and egg-bearing) were tagged and 400 were recaptured. Results showed an offshore migration in the fall to deep water (50 fathoms), and a return to shallow water in the spring, often to water less than 10 fathoms. Movement of broodstock in the summer was reduced and no clear patterns were determined. The majority of movements by the tagged broodstock were less than 30 miles.

Cowan et al. (2007) conducted an innovative study to determine the relationship between temperature, movement and body size for ovigerous lobsters. The delineation between small and large lobsters was 93 mm CL which is the size of 50% maturity in the Gulf of Maine. Results from this study showed that large egg-bearing females (>93mm CL) moved greater distances and were exposed to warmer temperatures in the winter than small egg-bearing females. However, the temperature profiles also showed that large lobsters experienced cooler water temperatures in the spring and thus the number of degree-days was similar between the two groups. It was also not clear from this study when the eggs that were being carried by these females hatched. A similar study by Goldstein and Watson (2015) in NH coastal waters demonstrated that the eggs carried by ovigerous females that moved offshore in the winter probably hatched before they moved back inshore in the spring/summer. They also determined that moving offshore did not, in fact, increase the number of degree days and rate of egg development in comparison to lobsters that remained inshore. Therefore, they hypothesized that these offshore movements might serve to place females in ideal locations for larval survival and ultimately, for settlement. Campbell (1990) reached similar conclusions as a result of studies in the Grand Manan region in Canada. Five different areas were sampled based on depth and substrate. Within the study area, consistently more egg-bearing females were caught in one of these areas and so he suggested that specific areas around Grand Manan may be ideal for egg extrusion/hatch due to warm mixed waters. He also theorized that the strong tidal currents in the area with a high abundance of egg-bearing lobsters may be ideal for rapid dispersal of newly hatched larvae.

Currents

It has been shown in various decapod crustaceans that egg-bearing females direct their movements to areas that might be conducive to larval survival. For example, Atlantic blue crabs *Callinectes sapidus*, mate in low salinity areas of estuaries and then females migrate into the lower/mouth of the estuary where eggs hatch into pelagic larvae that are carried by ebbing tides into higher salinity areas to complete metamorphosis (Tankersley, 1998). Fiddler crabs release their larvae at spring high tides to aid in the transport of zoea to primary estuaries where salinities are suitable for development (Epifanio, 1988). Similarly, female tanner crabs form aggregations and results suggest the crabs take advantage of tidal patterns to enhance larval hatch (Bradley 2003). It's possible that American lobsters may choose certain areas to release their larvae for the same reasons. Previous research has shown aggregations of large mature females in areas with strong currents (Campbell 1990, Robichaud and Campbell 1991). Additionally, Goldstein (2012) provided evidence that egg-bearing females may move offshore to hatch their eggs to aid in transport of larvae to optimal settling grounds. Larval drifters were utilized in that study to simulate the trajectory of larvae hatched offshore versus inshore. They found evidence to suggest the offshore trajectories were more suitable for larval survival, as inshore drifters tended to wash up on shore in short periods of time.

All of the aforementioned studies demonstrate the ability of mobile crustaceans to detect oceanographic factors which might influence the eventual survival of their young and then migrate to locations where conditions are optimal. In this study I first demonstrated that egg-bearing lobsters aggregate in certain areas around the Isles of Shoals (IOS), specifically the east side of the IOS, which is closer to deep water and has higher currents than the west side. Additionally, females with early stage eggs tend to inhabit shallow water areas, while those with eggs that are in the process of hatching are found in deeper water. This led to the hypothesis that egg-bearing females migrate to these deeper water areas just before their eggs are due to hatch and in the second chapter of my thesis I used ultrasonic telemetry to confirm this hypothesis.

CHAPTER 1

DISTIBUTION OF OVIGEROUS AMERICAN LOBSTERS NEAR THE ISLES OF SHOALS, NEW HAMPSHIRE

Abstract

Aggregations of egg-bearing (ovigerous) American lobsters, *Homarus americanus* (H. Milne-Edwards, 1837), have been documented throughout the species range, but it is not clear why they tend to accumulate in these areas. One such aggregation occurs near the Isles of Shoals (IOS), New Hampshire, USA. The overall goal of this study was to determine if reproductive status, depth, temperature and/or current might explain their presence in this area. In 2013 and 2014, research traps were fished at three depth strata (5-15, 16-25 & 26-35 m), on similar substrates, on both the eastern and western side of the IOS to quantify population demographics. Traps fished on the eastern side of the IOS caught significantly larger female lobsters and ~3 times more ovigerous lobsters than those on the western side. Interestingly, the catch rate of females carrying eggs that were hatching was significantly higher in the deep-water stratum (26-35 m) compared to shallow areas (5-15 m), when combining data from both sides of the IOS. In contrast, late stage pre-hatch animals were significantly more abundant in shallow water. Thus, it appears that female lobsters move to deeper water prior to hatching their eggs, and therefore, we hypothesize that lobsters accumulate in specific areas, like IOS, to brood their eggs in part because of their proximity to preferred deep water and high-current hatching locations.

Introduction

The commercial harvest of American lobster *Homarus americanus* (H. Milne-Edwards, 1837) in the United States occurs from Virginia to Maine, and has long been one of the most valuable single-species fisheries in the country. For example, in 2015 approximately 66,000 metric tons were landed, with an estimated value of 620 million dollars (NOAA 2015). If a resource of this importance is to be managed as a sustainable fishery it is imperative that regional populations are closely monitored and that we gain a better understanding of the factors that influence the distribution of reproductive female lobsters. Protection of egg-bearing lobsters (EBLs) is at the foundation of the lobster management pyramid (ASMFC 2006, ASMFC 2009, ASMFC 2015), and as climate change continues to affect the Gulf of Maine ecosystem (Mills et. al 2013), gaining a better understanding of the factors that influence their distribution is paramount.

Aggregations of egg-bearing American lobsters have been documented in the spring and summer throughout the species range, in the waters off Grand Manan, eastern Canada (Campbell and Pezzack 1986, Campbell 1986, Campbell 1990), around Georges Bank (ASMFC 2015, Henninger & Carloni 2016) and in specific areas in Southern New England (Glenn et al. 2011). Factors that may cause reproductive females to aggregate in these regions are still unknown, but it has been suggested that temperature, currents and/or substrate could play a role (Campbell 1990, Robichaud & Campbell 1991).

Lobsters can detect small changes in water temperature (Jury and Watson 2000) and, because they prefer certain temperatures and avoid others (Crossin et al. 1998), thermal gradients have a large influence on their movements and distribution (Cowan et al. 2007, Jury and Watson 2013). It has been suggested that seasonal inshore/offshore movements of females serve to increase the number of degree days for gonad development and synchronize their molt/reproductive cycles (Aiken and Waddy 1986, Campbell and Stasko 1986, Waddy and Aiken 1995, Crossin et al. 1998). It has also been shown that warm water accelerates development of eggs (Templeman 1940, Pandian 1970, Perkins 1972, Goldstein & Watson 2015), and there is evidence that egg-bearing lobsters are found in shallow water in the spring, perhaps to provide a sufficient amount of heat units/degree days for egg development (Campbell 1986, Campbell & Pezzack 1986, Campbell 1990).

One feature that characterizes some of the locations where EBLs aggregate is higher water currents (Campbell 1990, Robichaud and Campbell 1991), which have also been linked to aggregations of other decapod crustaceans. For example, dense aggregations of rock lobsters *Jasus edwardsii* were observed in several locations around New Zealand where there are strong tidal water movements, and the authors suggested this may facilitate rapid dispersal of newly hatched larvae (McKoy & Leachman 1982). Similarly, female Tanner crabs *Chionoecetes bairdi* aggregate in areas that may allow them to take advantage of tidal patterns for larval hatch (Bradley 2003). Though not linked to aggregating behavior, spiny lobsters (*Panulirus argus)*, Atlantic Blue crabs (*Callinectes sapidus*) and fiddler crabs also move to areas conducive for larval survival/dispersal prior to egg hatch (Epifanio 1988, Tankersley 1998, Bertelsen and Hornbeck 2009). Finally, recently Goldstein and Watson (2015) found that ovigerous lobsters that moved offshore in the fall did not return inshore in the spring, but remained there until their eggs hatched. This further suggests that ovigerous lobsters might seek these offshore areas because they are ideal for larval dispersal, due to the prevailing currents.

It has also been suggested that bottom habitat might be a factor influencing the distribution of EBLs, however it is often very difficult to separate bottom type from water depth. Lobster population demographics tend to differ based on substrate and geographic location. For example, in Massachusetts, Glenn et al. (2005) found that sex ratios varied by bottom type and depth. The mid-water and deep-water areas with complex bottom were dominated by females, while males dominated the shallow areas with featureless bottom. Sex ratios were close to 1:1 in the shallow complex, and mid/deep featureless bottom areas. This same study found no difference in size distribution by bottom type. In contrast, of the five areas Campbell (1990) sampled, ovigerous lobsters were most abundant in the shallow, sand/clay bottom, location. Whether egg-bearing American lobsters prefer specific substrates remains unknown, but substrate has been linked to aggregations of other decapod crustaceans. For example, Stone and O'Clair (2002) suggested that ovigerous Dungeness crabs aggregated in areas where unconsolidated fine sand provided a high rate of oxygen exchange for developing eggs.

Data from the New Hampshire Fish and Game Department's (NHF&G) Lobster Sea Sampling Program (LSS) has consistently shown a higher proportion of catch comprised of EBLs at the Isles of Shoals (IOS), compared to other coastal locations (NHF&G 2014). Furthermore, Goldstein and Watson (2015) recently demonstrated that EBLs migrate to areas near the IOS and remain there until their eggs hatch, suggesting there is something about this location that is favorable for egg development, egg hatching and larval survival. This study was undertaken to quantify lobster population demographics around the Isles of Shoals, with an overall goal of using the data obtained to identify potential factors, such as temperature, depth and currents that may influence the distribution and abundance of egg-bearing lobsters.

Materials and Methods

STUDY AREA:

Data from New Hampshire Fish and Game Department's (NHF&G) Lobster Sea Sampling (LSS) Program in 2011 & 2012 were used to determine areas with high concentrations (aggregations) of egg-bearing lobsters (EBL) within NH State waters. This fisheries-dependent monitoring program consists of observers sampling catch aboard commercial lobster vessels both coastal locations and at the Isles of Shoals (for procedures see NHF&G 2015). The abundance of EBLs was quantified in terms of catch per trap and these data were plotted in ARC View GIS to determine the spatial distribution and catch rate of EBLs at coastal locations compared to the Isles of Shoals. Based on these data, we focused our attention on areas around the Isles of Shoals (IOS), NH for this study (Fig. 1-1). This area is located approximately 10 km off the coast of NH/ME where depths range from 1 to 45 m. Substrate in the area is quite variable, ranging from hard bottom (ledge/boulder) to soft bottom (mud/sand).

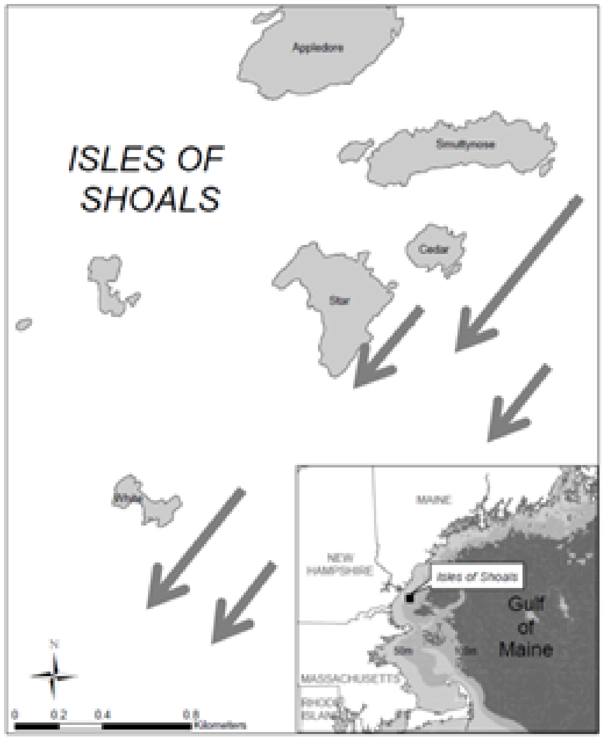

Figure 1-1. Map of study area (Isles of Shoals) located approximately 10 km off the coast of NH, USA. Black arrows depict the general direction of tides/currents in this area of the Southern Gulf of Maine.

DATA COLLECTION AND EXPERIMENTAL DESIGN:

Research trawls (traps tied to a common line) were then set in 2013 and 2014 with a specific emphasis on making comparisons between the abundance and sizes of EBLs on the east vs west sides of the IOS. Previous data collected from LSS Program showed a preponderance of egg-bearing lobsters on the eastern side of IOS compared to the west and so this study was designed to test that hypothesis. Three depth strata were chosen, with traps fishing in water that was 5-15, 16-25 and 26-35 m deep. Within in each depth stratum two sites were sampled, one on the west side and one on the east side. This translated to a total of six sites, three on the west side and three on the east side (Fig. 1-2). Trawls were fished at similar depths and on similar substrates on both sides of the IOS so that population demographic comparisons could be made between sites at the same depth. Substrate consisted of complex hard bottom for both shallow and mid-water strata on both sides, whereas in the deep stratum trawls were set on smooth gravel bottom due to the scarcity of complex bottom at depths > 30 meters in this area.

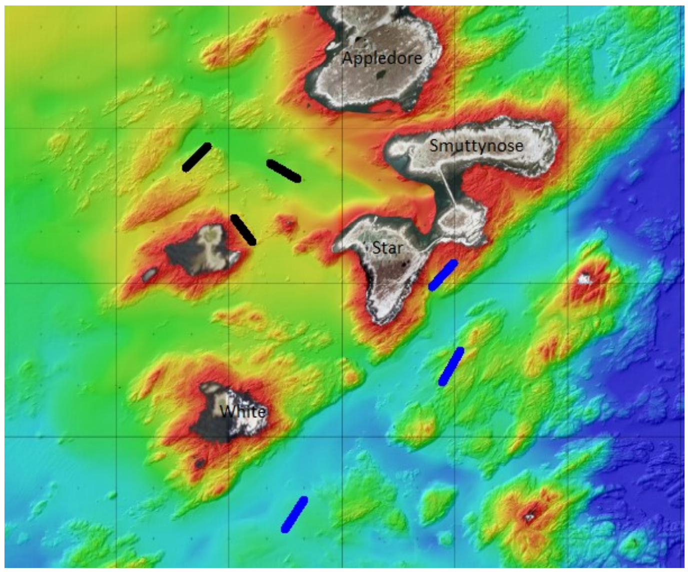

Figure 1-2   Location of trawls around the IOS. Black lines depict trawls on the west side and blue lines depict trawls on the east side. Trawls were fished at similar depths and substrates on both sides so comparisons could be made. Colors indicate depth gradient from shallow (1 m) to deep (50+ m): red, yellow, green, light blue and dark blue.

To ensure that traps were set on similar substrates on both sides of IOS three approaches were used to determine bottom type. First, bottom type was evaluated using multi-beam data collected by the University of New Hampshire (UNH) Center for Coastal and Ocean Mapping (CCOM), with backscatter to help determine substrate. Secondly, a drop camera was used to visualize the areas where traps would be set. Third, sonar was used to verify traps were, in fact, set on the intended substrate.

Trawls were hauled twice a month, on three night soaks, from June through August in 2013 and from May through August in 2014. The bait consisted of approximately 850 grams of Atlantic herring packed into 30.5 cm mesh bait bags. In 2013 each trawl consisted of two rectangular traps measuring 90 cm x 47 cm x 35 cm with two main compartments, a kitchen (where bait was hung) and a parlor; one trap did not have an escape vent (ventless trap) and one had a 4.9 cm x 12.7 cm escape vent. In 2014, two additional traps were added to each trawl (one vented and one ventless).

BIOLOGICAL DATA AND TAGGING:

When traps were hauled the carapace length (CL) of each lobster was measured to the nearest millimeter (mm) with calipers and egg condition was assessed for all ovigerous lobsters. Eggs were assigned to one of six different stages based upon a modified version of the system used by Helluy and Beltz (1991), so that we could estimate when they would hatch. Egg staging also included the determination of eggs that were in the process of hatching, which generally occurs in this region from June-August. Egg staging also allowed us to better understand if the depth distribution of EBLs was related to different developmental stages of their eggs. A full description of the egg staging technique used in this study can be found at https://www.youtube.com/watch?v=6r6PkSCQ8iU&feature=youtube. To quantify recapture rates in 2013 all lobsters were banded with color bands around the carpus segment and female lobsters >70mm were tagged with T-bar style tags. In 2014 all egg-bearing lobsters were tagged. Less than one percent of the tagged lobsters were recaptured in research traps in both years combined.

ENVIRONMENTAL DATA:

Bottom temperature was monitored with Onset HOBO data loggers in both 2013 and 2014 at all sites. Additionally, SeaHorse tilt current meters developed by Sheremet (http://www.nefsc.noaa.gov/epd/ocean/MainPage/tilt/shtcm.html) were affixed to some traps on both sides of the IOS in the shallow and mid water strata in 2013.

ADDITIONAL SURVEYS:

Two NHF&G surveys were conducted during a similar time period along the NH coast by the lead author and fisheries technicians. These surveys were part of the LSS Program and Random Depth Stratified Ventless Trap Survey (RSVTS). Data from these surveys were used to corroborate results from IOS research traps with regards to depth related hatching patterns. For procedures on both coast wide surveys see NHF&G 2015. Only the shallow and deep water strata were used for IOS Research Traps in this analysis for two reasons: 1) these depths matched more closely with the depth delineation from the abovementioned surveys and; 2) the mid-water stratum did not fit with either of the two more extreme depth strata.

DATA ANALYSES:

The main objective of this study was to compare the lobster population demographics between the west and east side of the IOS and explore potential factors that might lead to these differences. Comparisons were made between lobsters captured at different depth strata on both sides and, where appropriate, these data were grouped by side and comparisons were made between the east and west. Trawls were set up exactly the same (i.e. configuration of traps, vents, spacing between traps) at each location so comparisons could be made between sites within years. We used both vented and ventless traps on each trawl to more accurately assess population demographics, a method similar to the coastwide RSVTS conducted throughout New

England (ASMFC 2015). These trawls were treated as “units” for the purpose of comparisons between sites. Although we realize selectivity is different between vented and ventless traps, we only made comparisons between trawls set up exactly the same with the assumption of equal catchability between each trawl. Temperatures were similar on both sides of the island within each depth stratum (see results section 3.5).

Catch rates were analyzed in terms of catch per trap haul (CPTH, which is also referred to as catch per unit effort, or CPUE), where the total number of lobsters captured in each trawl was divided by the total number of traps in the trawl. Some analyses were carried out only for female lobsters ≥83 mm for two reasons: 1) this is the minimum legal size that lobsters may be harvested inshore in the Gulf of Maine and; 2) because this is the estimated size at which 50% of animals are sexually mature in this area (Watson et al. 2017).

Where data satisfied normality assumption, Student’s t-test was used to compare distributions. In cases were data did not meet normality assumption, but had equal variance, a non-parametric Wilcoxon’s test was conducted. Where data did not meet normality assumption and had unequal variance, Mood’s Median test was used. A generalized linear model was used to assess differences in catch rate of egg-bearing lobsters by side and depth which included an interaction term between both variables. Finally, due to small sample sizes, data from 2013 and 2014 were pooled for the catch rate by egg stage/depth analysis. Prior to pooling, it was determined that both years showed similar trends and no significant difference existed between catch rate distributions by year as assessed via Kolmogorov Smirnov test. All data were analyzed using the statistical software package JMP Pro 12.1.0.

Results

SIZE DISTRIBUTION:

Based on NHF&G Sea Sampling data, the abundance of EBLs at the IOS was significantly higher ($P<0.05$, unpaired t-test) than the coastal location and thus we conducted our study there (Figure 1-3). A total of 2,295 lobsters were sampled from research traps in 2013 (n=701) and 2014 (n=1594); 1,030 from sites on the east side and 1,265 from the west side. Overall, lobsters on the east side were significantly larger than those on the west side when making site to site comparisons within each depth stratum (Fig. 1-4; $P<0.05$, unpaired t-test). Females on the east side were significantly larger by depth for both years (Fig. 1-5; $P<0.05$, unpaired t-test). The mean CL for males was larger on east side by depth, but generally these differences were not significant (Fig. 1-5, unpaired t-test). In general, the median CLs of females carrying eggs, or showing signs of recently hatched eggs, were larger on the east side, but there was no significant difference (Table 1; Moods Median Test, $P>0.05$), however, when combining years and depth strata, lobsters on the east side were significantly larger ($P<0.05$, Mood's Median Test).

Table 1. Comparison of median size (mm) of females with eggs, or with signs of recently hatched eggs, by depth stratum and site in 2013 and 2014.

Year	Depth Stratum	Site	n	Median	Location	N	Median	P-value
2013	Shallow	East	11	79.0	West	6	80.0	P>0.05
2013	Mid	East	16	92.0	West	10	83.5	P>0.05
2013	Deep	East	14	84.0	West	6	81.5	P>0.05
2014	Shallow	East	48	81.0	West	15	81.0	P>0.05
2014	Mid	East	50	83.5	West	17	81.0	P>0.05
2014	Deep	East	43	83.0	West	11	80.0	P>0.05

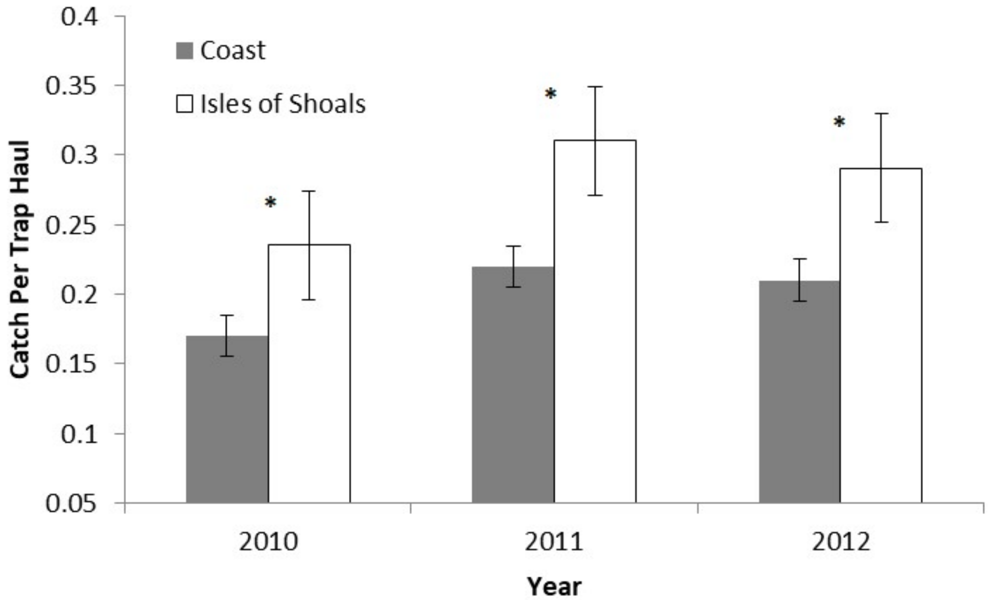

Figure 1-3. Catch per trap haul comparison of two NHF&G Sea Sampling locations by year. Means here, and in subsequent figures, are expressed as ± SEM and asterisks (*) denote a statistically significant difference (P<0.05).

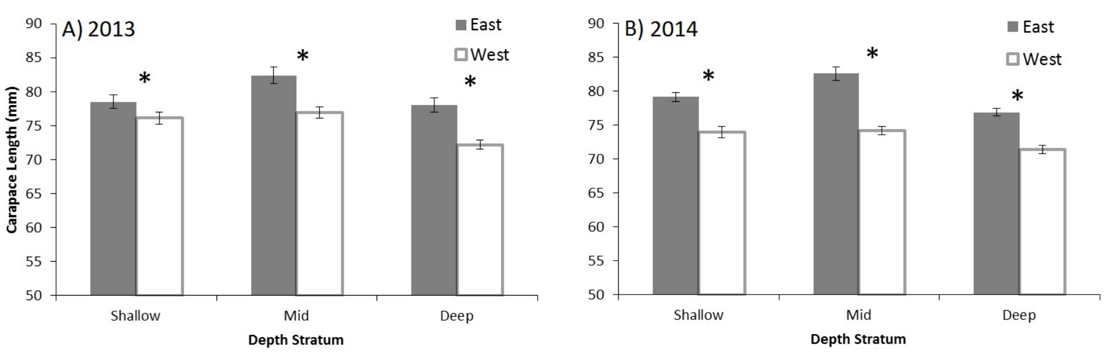

Figure 1-4. Mean carapace length (mm) of lobsters sampled from research traps at the Isles of Shoals in (A) 2013 and (B) 2014. Sample size (n) for all sites is >75.

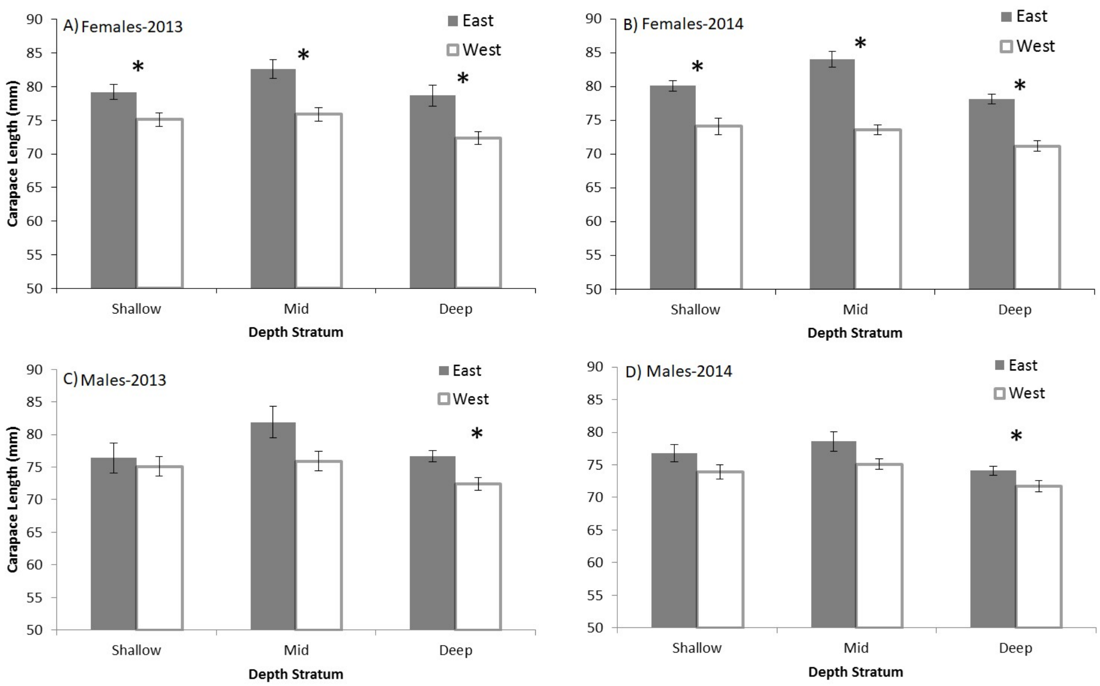

Figure 1-5. Mean carapace length (mm) of female (top) and male (bottom) lobsters sampled from research traps at Isles of Shoals in (A) & (C) 2013 and (B) & (D) 2014. Sample size of females (n) for all sites is >50, while sample size for males for all sites is ≥19 in 2013 and ≥45 in 2014.

PERCENTAGES:

Sex ratios were female skewed on the east side in each depth stratum for both years (Fig. 1-6). The sex ratio for all lobsters in 2013 on the east side was 69% female compared to 54% on the west side. Similarly, the sex ratio was higher in 2014 on the east side (72% female) compared to the west (56%). The greatest disparity in sex ratio between the two sides was for lobsters ≥ 83 mm CL. From 2013-2014, 78-84% of lobsters (≥ 83 mm CL) were female on the east side vs 36-42% on the west side.

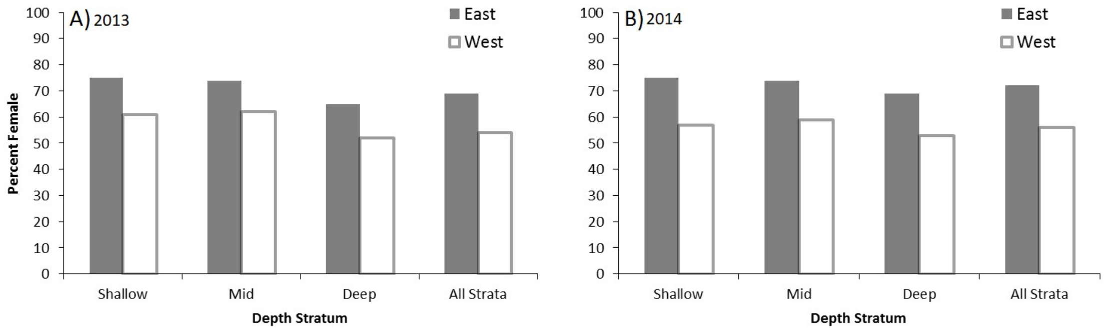

Figure 1-6. Comparison of sex ratios (% female) between the east and west side of the Isles of Shoals for lobsters sampled in (A) 2013 and (B) 2014, from three different depth strata (shallow, mid & deep), as well as all strata combined. There were a higher percentage of females captured on the east side in each depth stratum for both 2013 and 2014.

CATCH:

There were no significant differences in the catch rates of female lobsters by depth stratum in either year (Fig. 1-7). There was, however, a significantly higher catch rate of females ≥ 83 mm CL on the east side in the deep water stratum in 2013 and for all three strata in 2014 ($P<0.05$, Wilcoxon). Additionally, the catch rate of EBLs was 3.2 times higher on the east side. A generalized linear model was constructed using depth (shallow, mid & deep), side (east/west) and interactions (side & depth) as effects and CPTH as a response variable for EBLs in both years. Side was shown to be significant and depth was not significant; indicating catch rates of EBL were generally lower and uniform by depth on the west side and higher and uniform by depth on the east side (Fig. 8; GLM, $P<0.05$). Furthermore, there was no significant difference between the catch rates of all egg stages combined by depth on the east or west side ($P<0.05$, unpaired t-test).

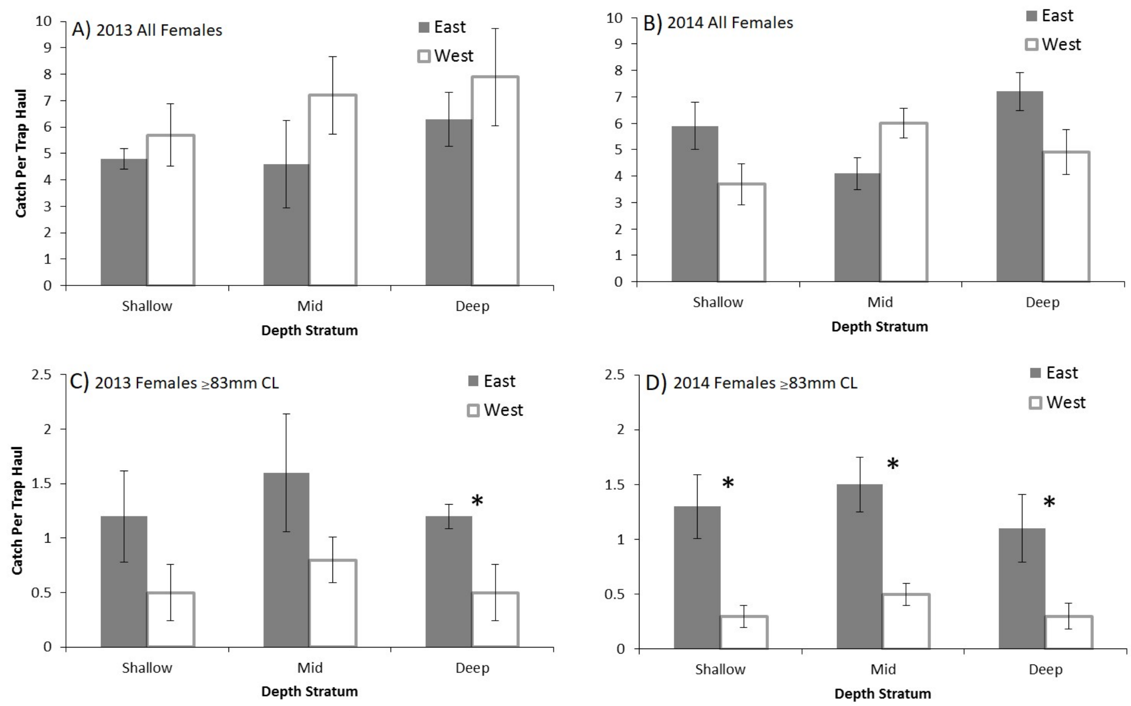

Figure 1-7. Catch rate comparison of female lobsters sampled from research traps at Isles of Shoals in (A) & (C) 2013 and (B) & (D) 2014. Top is all females and bottom graphs are just legal females (≥ 83mm CL).

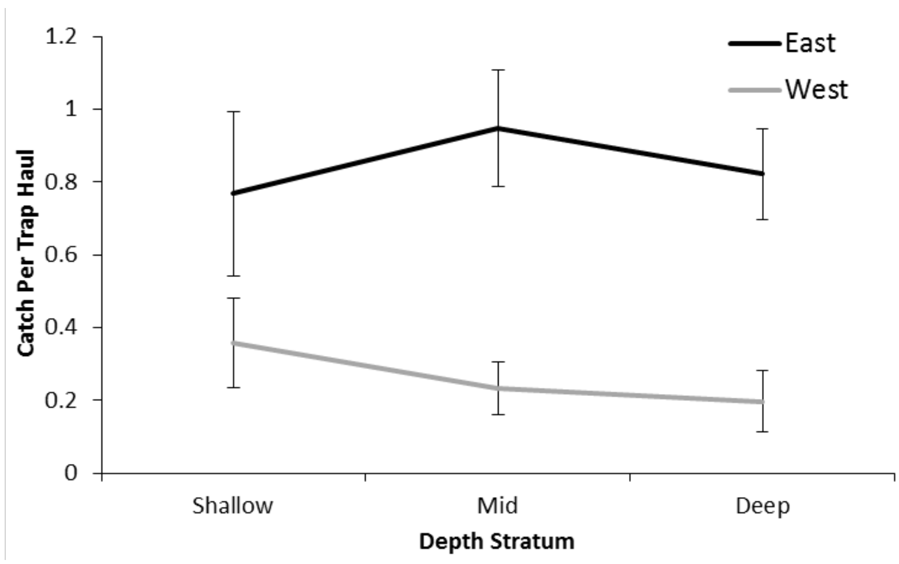

Figure 1-8. Generalized linear model illustrating that catch rates of EBLs on the east side of IOS were relatively high and uniform by depth compared to the west side where catch rates are low and uniform. The significant term effecting catch per trap haul in the GLM was side, $P<0.05$.

CATCH OF LATE STAGE PRE-HATCH EGGS VS EGGS IN PROCESS OF BEING HATCHED:

Mean CPTH of EBL in the process of hatching eggs and those with late-stage pre-hatch eggs varied by depth. The CPTH for pre-hatch lobsters was significantly higher in the shallow depth stratum (both sides combined) compared to the deep water stratum (Fig. 1-9, Wilcoxon, $P<0.05$). In contrast, the CPTH of EBLs in the process of hatching eggs was significantly higher in deep water (both sides combined) compared to shallow (Fig. 1-9, Wilcoxon, $P<0.05$). A similar pattern was observed for the NHF&G's LSS Program (shallow <21 m, deep >21 m) and for the NHF&G's RSVTS (Shallow=<20vm, Deep >40 m). LSS Program data yielded a significantly higher catch rate of pre-hatch lobsters in shallow water and a significantly higher catch rate of hatching lobsters in deep water (Fig. 1-9, Wilcoxon, $P<0.05$). The RSVTS data also showed a higher catch rate of pre-hatch EBLs in shallow water, but the difference wasn't significant (Wilcoxon, $p>0.05$). Finally, the catch rate of EBLs in the process of hatching from the RSVTS was ~16 times higher in deep water (Fig. 9, Wilcoxon, $P<0.05$). These data, taken together, suggest that lobsters carrying eggs that are about to hatch move to deeper water.

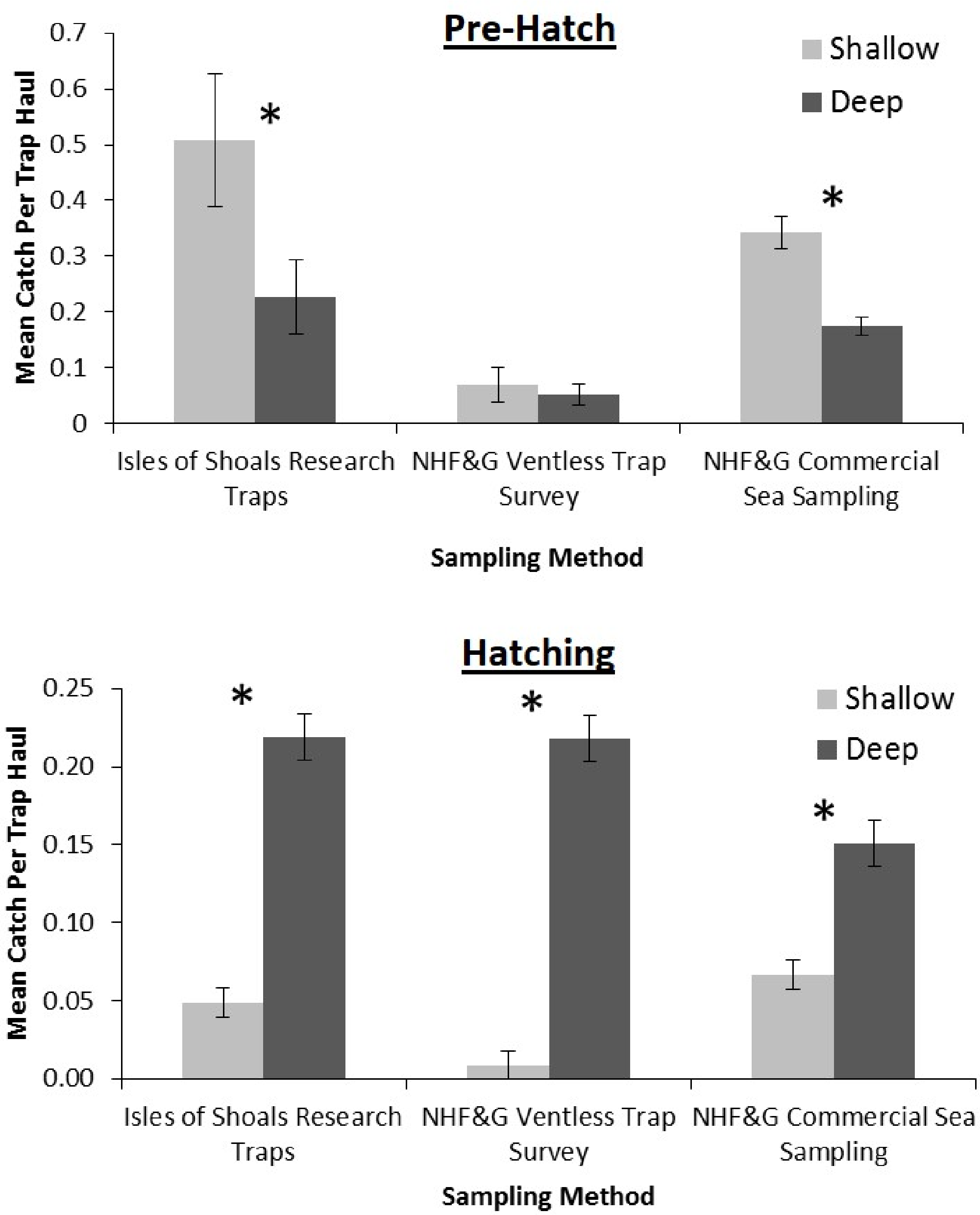

Figure 1-9. Catch rate of pre-hatch late stage egg-bearing lobsters (top) and egg-bearing lobsters in the process of hatching eggs (bottom) by depth and sampling method. Catch rates of pre-hatch lobsters were higher in shallow water, while catch rates of lobsters in the process of hatching eggs were significantly higher in the deep water with all three sampling methods.

ENVIRONMENTAL DATA:

Mean water temperatures (^{0}C) in the shallow and mid-depth strata were similar on both sides of IOS (shallow: east $\bar{x}$=11.7 ± 0.94, west=$\bar{x}$ 11.3 ± 0.10; mid-depth stratum: east $\bar{x}$=9.9 ± 0.11, west=$\bar{x}$ 9.8 ± 0.07). In the deep water stratum the average for the east side was 1^{0}C colder than the west (east $\bar{x}$=8.4 ± 0.07, west=$\bar{x}$ 9.4 ± 0.07). However, current speeds (cm/s) were generally stronger and more variable on the east side of the IOS for both the shallow and mid-depth strata (Fig. 1-10). These data indicate the currents, rather than water temperatures showed a greater disparity between the east and west sides of IOS and thus might have a larger impact on the distribution of females.

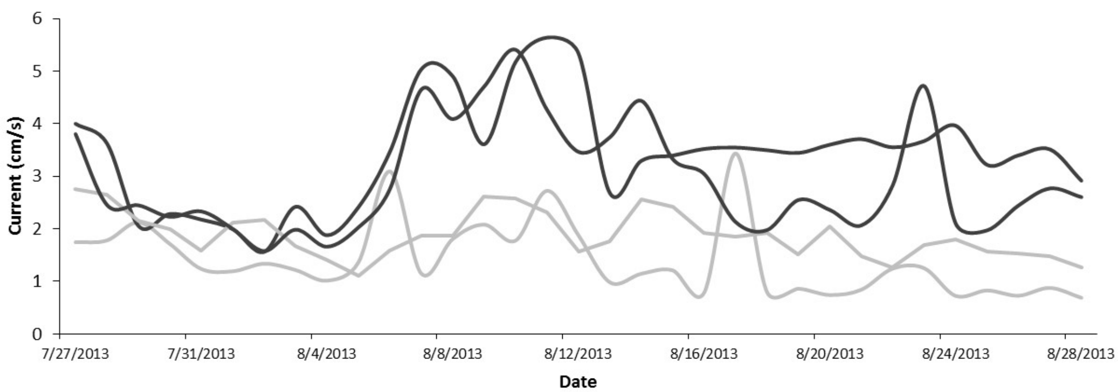

Figure 1-10. Currents (cm/s) at the shallow and mid-water strata on both sides of the Isles of Shoals in 2013. The sites on the eastern side of the IOS are depicted in black; the gray lines represent the sites on the west. Generally current speeds on the east side are higher and more variable than on the west side.

Discussion

Results from this study demonstrate differences between lobster population demographics on the east and west side of the Isles of Shoals. Females, but not males were significantly larger on the east side for all three depth strata, and a higher percentage of lobsters on the east side were female. This disparity in sex ratios was particularly compelling for lobsters ≥83 mm CL, that made up 78-84% of the sampled population on the east side in 2013 and 2014, respectively. The most recent estimates of size at maturity in this area show that ~50% of females are mature at 83 mm CL (Watson et al. 2017). In addition, egg-bearing lobsters were significantly more abundant on the east side in all three depth strata. These data, taken together, suggest that differences in the spatial distribution of female lobsters near the IOS are likely to be related to sexual maturity and reproduction.

Past studies have shown a similar pattern in the distribution of egg-bearing lobsters. Specifically, Campbell (1990) found that a specific area around Grand Manan, Canada had a higher abundance of egg-bearing lobsters. He theorized that lobsters may aggregate in shallow water due to warmer temperatures and/or to be near currents that may aid in larval dispersion during egg hatch. In our study we differentiated between females carrying eggs that were pre-hatch, but would hatch that season, and those carrying eggs that were in the process of hatching. This allowed us to determine catch rates associated with both developmental stages. We found that females carrying late-stage pre-hatch eggs were significantly more abundant in shallow water compared to the deep water when combining data from both sides of the IOS. These shallow areas were also on average 2 to 3°C warmer than the deeper locations. Therefore, these data are consistent with Campbell's hypothesis that egg-bearing females prefer areas that are warmer in the spring/summer (Campbell 1986, 1990). This preference for warmer water is likely related to the fact that warm water, especially water that is rapidly warming in the spring (i.e. March-May), accelerates egg development (Goldstein and Watson 2015) and therefore lobsters move to these areas in the spring to take advantage of the thermal properties.

Temperature appears to explain some of the disparity between the abundance of late-stage pre-hatch egg-bearing lobsters in the shallow water areas compared to deep areas, however, since water temperatures at each depth stratum were similar between the two sides of the IOS, thermal differences do not explain the disparity in sex ratios and catch rates of EBLs between the two sides of the IOS. Our data showed a higher abundance of EBL on the east side, which is also the side that is closer to deep water. As mentioned above, our results support the generally accepted paradigm that EBLs are found in warm shallow water in the spring, potentially to accelerate development of their embryos. However, unlike previous research on this topic, we found that females in the process of hatching eggs were significantly more abundant in the deep stratum compared to the shallow water stratum, suggesting they might move there just prior to hatching. This, to our knowledge, is the first study to provide evidence of movement to deep water around the time eggs hatch. The seasonal reproductive movements inferred from our study suggest movement to warm shallow water in the spring to brood eggs, followed by movement back to deep water prior to hatching eggs. To accomplish both of these biological migrations, a shoal area with steep bathymetry located offshore may be ideal. Although the entire IOS have these general characteristics, when comparing bathymetry of the east location to the west, the east is closer to deep water (Fig. 1-2) and would presumably allow lobsters to undertake these seasonal migrations with the least amount of energy expenditure. Similar aggregations have been documented in offshore shoal areas throughout the Gulf of Maine and Georges Bank

(Campbell and Pezzack 1986, Campbell 1986, Campbell 1990, Henninger & Carloni 2016), underlining the importance of these areas to female reproduction.

Our current hypothesis is that female lobsters move from shallow to deep water just prior to hatching their eggs which may provide an optimal location for larval dispersal and survival. The data supporting this hypothesis are as follows: First, pre-hatch egg-bearings lobsters are more common in the shallow water, but significantly more females in the process of hatching eggs were captured in the deep water areas, which we do not feel can be attributed to differences in catchability by temperature or substrate as we found no significant difference in catch rate by depth for all egg stages combined. Second, in both the LSS Program and RSVTS, lobsters in the process of hatching eggs were significantly more abundant in the deep water compared to the shallow areas. Finally, preliminary acoustic tracking data with EBLs in the same area indicate that the majority of the animals tagged moved from shallow to deep water before their eggs began to hatch (Carloni et al 2018). While past research has suggested ovigerous lobsters take part in rapid movement after their eggs have already hatched (Jarvis 1989, Watson and Howell 1999), this is the first study with American lobsters indicating that females move to different areas just before eggs hatch.

Previously it has been suggested that ovigerous females seek out places with high currents that would aid in larval dispersal (Campbell 1990, Robichaud and Campbell 1991, Goldstein and Watson 2015), which appears to be the case in some other decapod crustaceans as well (Epifanio 1988, Tankersley 1998, Bertelsen and Hornbeck 2009). Currents in the western GOM are dominated by the Western Maine Coastal Current (WMCC), which tends to move in the southwest direction (Fig. 1). The west location in our study sits behind Appledore Island and may not be as exposed to the dominant currents in the area due to local bathymetry; which was substantiated by our current measurements in 2013. Thus, the stronger currents on the east side of the IOS may be attractive to lobsters, because if eggs were to hatch there, the larvae would more likely be exposed to the strong prevailing southwest currents, which would carry them parallel to the coast towards Massachusetts.

Goldstein and Watson (2015) found that American lobsters that moved offshore near the Isles of Shoals in the fall, stayed offshore through the time the eggs were assumed to hatch and suggested that the survival and eventual settlement of larval lobsters would be enhanced in areas away from shore, due to prevailing currents. Additional evidence for this hypothesis may be found in the Gulf of Maine Coastal Current (GMCC) which is centered along the 100 meter isobath and extends to within 10 km of the coast (Churchill et al. 2005). Eggs hatched closer to shore and farther away from this predominant current are projected to provide more of a local source of recruitment than those hatched farther offshore within the coastal current (Incze and Naimie 2000, Incze et al. 2010). The benefits of dispersal farther away from parent stock for this species are unknown at this time; however this current may simply provide larvae with a lower likelihood of stranding on the shoreline. Though passive drifters likely oversimplify larval transport dynamics, some general observations are worth noting: Drifters released near the IOS showed general trajectories to the southwest along the shore, eventually reaching areas that are presumably good for settlement after ~30 days, whereas those released near shore were often transported towards the coastline (Goldstein 2012).

It is also possible eggs hatched offshore closer to the GMCC may encounter a higher abundance of food for larval development. It has been proposed that the GMCC is the main transport of *Calanus finmarchicus* (Runge et al. 2015), a food source which has recently been linked to lobster postlarval abundance in the area (Carloni et al. in press). The abundance of this potential food source decreases closer to shore (Runge et al. 2012). So it may be beneficial to hatch larvae in closer proximity to this predominant current not only for optimal dispersal, but also for a consistent source of food. In the laboratory, larval lobster survival and rate of development to the postlarval stage has been reported to be strongly linked to food quality and quantity (Eagles et al. 1986). The function of this observed movement to deep water certainly requires additional research, but our data suggest that prevailing currents may have an effect on where and when lobsters brood their eggs, and where they are located when their eggs hatch. This, in turn, most likely has a strong influence on larval dispersal, survival and settlement.

Taken together these data provide evidence that egg-bearing lobsters aggregate in certain areas and that currents and proximity to deep water may play a role in their distribution. Additionally, our data demonstrate that some ovigerous American lobsters move to deeper water just before their eggs hatch. Based upon these data and past studies, we believe these movements may provide optimal conditions for larval survival and dispersal. However, it is possible that egg-bearing lobsters hatch their eggs in deeper water to avoid rocky shoal areas that harbor finfish predators such as cunner, which are known to feed on early stage larvae (Herrick 1895). Alternatively, since stage I larvae are not very mobile and thus may be more vulnerable to predators, it may be beneficial to release them in deep water to give them more time to develop before eventually making it to warmer surface waters where a higher abundance of visual predators exist. Research is currently underway to both determine the adaptive significance of these movements and the environmental cues that guide these migrations.

CHAPTER 2

MOVEMENT AND ACTIVITY PATTERNS OF ACOUSTICALLY-MONITORED EGG-BEARING AMERICAN LOBSTERS AT THE ISLES OF SHOALS, NEW HAMPSHIRE

Abstract

Extensive research has been conducted on egg-bearing (ovigerous) American lobsters over the past several decades, and, it has generally been accepted that these animals move from deep offshore areas to shallow water in the spring to brood and hatch eggs. In Chapter 1, we found evidence that indeed, pre-hatch ovigerous lobsters were more common in shallow water; however, surprisingly we found females in the process of hatching eggs were more common in deeper (>30 m) areas. In 2016 and 2017 we monitored a total of 12 egg-bearing lobsters (AvgCL=96.2) with acoustic transmitters during the late-stage brooding and hatching season to test the hypothesis that these lobsters move to deeper water prior to hatching their eggs. We found that 92% of lobsters (n=11) moved to deeper water prior to the time their eggs were estimated to hatch. Of these, 25% hatched eggs within the array, while 67% left the array generally in a south southwesterly direction towards deep water. Results from Chapter 1 and Chapter 2 taken together, suggest that egg-bearing lobsters move to deep water prior to hatch which may be beneficial for dispersal and survival of hatched larvae.

Introduction

In the U.S., American lobster *Homarus americanus* (H. Milne-Edwards, 1837) is managed by the Atlantic States Marine Fisheries Commission (ASMFC) in cooperation with both state and federal agencies. Protection of egg-bearing lobsters (EBLs) has long been an effective management strategy (ASMFC 2006, 2009, 2015, Lebris et al. 2018) and although there has been extensive research conducted on this segment of the population (Saila and Flowers 1968, Campbell 1986, Waddy and Aiken 1995, Estrella and Morrissey 1997, Watson et al. 1999, Cowan et al. 2007, Goldstein and Watson 2015a), little is known about their activity and movement around the time of egg hatch. The location of these individuals during this critical period determines the release point of stage I larvae, and thus, directly affects the eventual area where postlarvae will settle. Furthermore, as climate change continues to affect the Gulf of Maine ecosystem (Mills et. al 2013), gaining a better understanding of these movements is critical to determining how larval dynamics and recruitment could change under different climate scenarios.

Results from passive tagging studies have demonstrated shallow-to-deep water migrations, with recaptures in warmer shallow water during the egg development/hatching season and deep water in colder months when both activity and egg development rates are low (Uzmann 1977, Campbell 1986, Steneck 2000). It has been hypothesized that these movements serve to increase the number of degree-days for embryo development (Templeman 1940, Uzmann 1977, Perkins 1972, Talbot and Helluy 1995). Collectively, these findings set the stage for the widely accepted paradigm of offshore-onshore migration patterns, which in turn implies that a majority of larvae for coastal populations are released inside the 50 m isobath near the coastline (Incze et al. 2010). Bio-physical modeling and drifter studies have demonstrated the location where eggs hatch can significantly affect the eventual location of postlarval settlement. Eggs hatched offshore are transported farther away from parent stock than those hatched closer to the shoreline (Inzce and Naimie 2000, Incze et al. 2010, Goldstein 2012).

In a study conducted close to this study's work, Goldstein and Watson (2015a) found that American lobsters that moved offshore near the Isles of Shoals, NH in the fall, stayed offshore through the time their eggs were presumed to hatch. This study theorized that the survival and eventual settlement of larval lobsters would be enhanced in areas away from shore, due to prevailing surface water currents. More recently, Carloni and Watson (2018) found high densities of egg-bearing lobsters near the Isles of Shoals (a group of Islands located 7 km from the NH coast, Chapter-1), and a higher abundance of these egg-bearing females on the eastern side of the islands, in close proximity to deep water and associated strong coastal currents. Moreover, they found that pre-hatch egg-bearing lobsters were more common in shallow water, but significantly more females in the process of hatching eggs were captured in deep areas, suggesting movement to deep water prior to hatch. Taken together, these findings suggest that American lobsters might undertake a reproductive migration just prior to when their eggs would hatch. This likely has an influence on larval transport dynamics because larvae are hatched in deep areas near prevailing currents.

It has been demonstrated that other species of marine decapod crustaceans migrate to areas favorable for larval survival and transport. For instance, spiny lobsters migrate to fore reefs to hatch eggs and move back to the same patch reef after their eggs have hatched (Bertelsen and Hornbeck, 2009). Atlantic blue crabs (*Callinectes sapidus)* mate in low salinity areas of estuaries and then females migrate towards the lower- estuary (i.e., tidal creek mouths) where eggs hatch and are transported into higher salinity areas which are required for metamorphosis into the megalopae stage (Tankersley, 1998). Additionally, fiddler crabs release their larvae at spring high tides to aid in the transport of zoea primarily into estuaries where salinities are sufficient for development (Epifanio, 1988). Thus, it is well documented that some decapod crustaceans display directed movements to areas favorable for larval dispersal, development, and survival. Furthermore, evidence is mounting that the same may be true for the American lobster (Campbell 1990, Goldstein and Watson 2015a, Carloni and Watson 2018). The main goal of this study was to more rigorously test this hypothesis by using ultrasonic telemetry to track the movements of late-egg stage berried females before, during, and after the time when their eggs hatch.

Methods

STUDY SITE:

Based upon results from Carloni and Watson (2018), this study was conducted on the eastern side of the Isles of Shoals, NH (Figure 2-1). This is a group of Islands located ~ 10 km from the NH coast, near the 50 meter isobath. The bathymetry in this area changes abruptly with depths ranging from 1 to 50 meters and is comprised of rocky reef complex and a mixture of gravel, sand and other fine sediments. Currents in this area are dominated by the Gulf of Maine Coastal Current (GMCC) which flows in a southwesterly direction, is centered on the 100 meter isobath and extends to within ~10 km of shore (Churchill 2005).

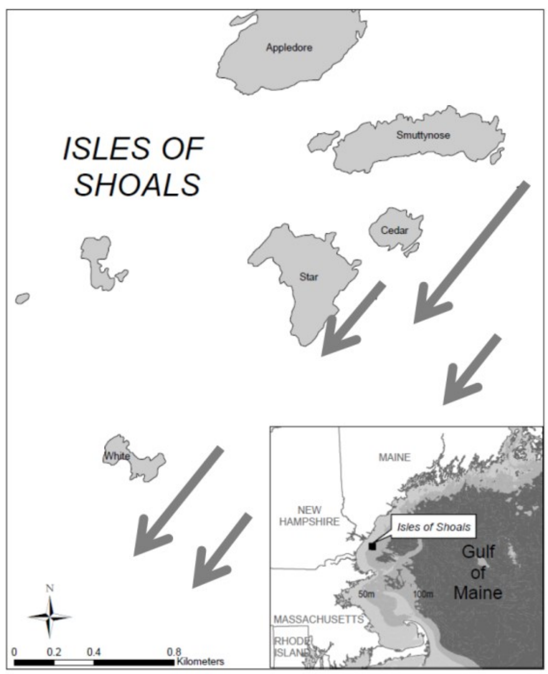

Figure 2-1. Map of study area (Isles of Shoals) located approximately 10 kilometers off the coast of NH, USA. Black arrows depict the general direction of currents in this area of the Southern Gulf of Maine.

ACOUSTIC TAGGING:

Egg-bearing lobsters were caught using standard lobster traps (dimensions= 40” x 21” x 16”, single parlor) fished at a depth of 14 m. Upon capture, lobsters were held onboard a research vessel at ambient water temperatures in a live-well for less than thirty minutes until they were fitted with acoustic transmitters.

Lobsters were fitted with Vemco V13AP coded tags (69kHz, 13mm diameter, 36 mm long, 6 g in water, VEMCO AMIRIX Systems), which recorded both pressure (depth in meters) and acceleration (activity, m/s^{-2}). VEMCO accelerometers output a digital value that represents an average level of activity over a sampling period in units of m/s^{-2} (m/s-2= $\sqrt{X2} + Y2 + Z2$). Immediately after the V13AP tag transmits depth, the tag begins sampling raw acceleration data from each of the XYZ axes at 10Hz for a period of 27 seconds and outputs an average level of activity; this was conducted on 90 second intervals. Ultrasonic tags were secured as described in Goldstein & Watson (2015), with special care given to placement of each tag in a consistent location and orientation on each lobster. Additionally, disk tags were attached dorsally to each lobster with text that read, “please release” with contact information for fishermen to report recapture information. The entire tagging process took 3-5 minutes and lobsters were placed back into the live well after tagging.

Eggs were visually inspected and staged in the field based upon a modified version of the system used by Helluy & Beltz (1991), which is described in detail at https://www.youtube.com/watch?v=6r6PkSCQ8iU&feature=youtube. We conducted the visual inspection to ensure eggs were in a late developmental stage and would hatch within the current year. Additionally, a small sample (20-25 eggs) was removed from each clutch and placed in a

2.0 ml tube containing 4% formalin-seawater fixative for later determination of a more precise estimate of hatch time, based on the Perkins Egg Index (Perkins 1972). Morrissey (2016) found no difference between actual and predicted weekly hatch times for lobsters kept in the lab.

Once all animals had been tagged, we placed them into a volitional cage with an opening at one end and lowered it to the sea floor at the original location of capture (14 m). The depth of release was verified via data from the acoustic telemetry array.

ENVIRONMENTAL DATA:

Bottom temperature and light were monitored with Onset HOBO data loggers in both 2016 and 2017 to provide a sense of the difference between shallow (14 m) and deep water (37 m) in the area. Additionally, daily mean wave height was downloaded from NERACOOS buoy BO1 (http://www.neracoos.org/datatools/realtime/all_data) on the Western Maine Shelf to identify potential storm events that could possibly promote movement of lobsters to deep water.

ARRAY DESIGN:

Prior to tagging, five omni-directional VR2W (VEMCO AMIRIX System) acoustic receivers were placed at varying depths throughout the study area. Receivers were placed approximately 400 meters apart and moored to the bottom via lobster traps weighted with lead bricks. Each receiver was attached to the buoy line via a gangion (short piece of rope) with a 23 cm trawl float which kept the receiver upright ~3 m off the bottom. Receivers recorded tag number, depth (m), mean acceleration (m/s^{-2}), date and time to the nearest second.

DATA PROCESSING:

Accelerometry-Accelerometer readings were averaged for each hour (0:00-23:00). Based on Jury et al. (2018) and results from this study, levels of activity below a threshold of 0.2 m/s^{-2} were determined to indicate limited movement, such as shifting around inside of a shelter or grooming activity. We did not remove these data from our analysis as they represent a form of activity and are part of the distribution of values; however, in activity plots 0.2 (m/s^{-2}) was identified to indicate limited activity (Jury et al., 2018). To determine if these lobsters were more active at night than during the day, we first determined the number of hours of light and dark, based on sunrise and sunset times (https://www.weather.gov/mrx/sr_ss), and then ran a non-parametric Wilcoxon's test for significance at the alpha 0.05 level between the two factors. We used Wilcoxon's test as data didn't satisfy normality assumption based upon Shapiro-Wilk test. Additionally, we used the HOBO light logger (lumens/ft^2) to provide an index of light intensity, expressed as an hourly mean from 6/16/2016-7/20/2016.

Depth- The average depth for each lobster during each day was and plotting to visualize if lobsters changed depth before, during or after their eggs were about to hatch. To determine change in depth, the daily mean depth before and after lobsters initiated movement to deep water was analyzed to determine rate of change in terms of percent.

Lobster positions-Average hourly positions were calculated for each lobster based upon an algorithm developed by Simpfendorfer et al. (2002). These estimated positions were determined based on the probability that a single omni-directional receiver will log a transmitter given the distance between the transmitter and the receiver, using the equation below. Note, this was done for each receiver and the example just shows a computation for two different receivers.

$$\frac{Lat(receiver\ \boldsymbol{A}) \times (\#of\ detections\ of\ ID)}{Total\ Detections\ for\ All\ rcvrs\ of\ ID} + \frac{Lat(receiver\ \boldsymbol{B}) \times (\#of\ detections\ of\ ID)}{Total\ Detections\ for\ All\ rcvrs\ of\ ID} = weighted\ average\ position$$

$$\frac{Long(receiver\ \boldsymbol{A}) \times (\#of\ detections\ of\ ID)}{Total\ Detections\ for\ All\ rcvrs\ of\ ID} + \frac{Long(receiver\ \boldsymbol{B}) \times (\#of\ detections\ of\ ID)}{Total\ Detections\ for\ All\ rcvrs\ of\ ID} = weighted\ average\ position$$

<u>Assumptions:</u>

1) The method assumes all receivers are detecting transmitters equally well, even though receivers can experience different conditions which can impact receiver performance.
2) Transmitter collisions can also bias data. This is a concern if there are a large number of tags present around one receiver for a given period of time.
3) It is assumed that all transmitters have a clear line of sight to receivers, so any transmitter being shadowed will result in a bias.

We used this method to estimate general paths of movement of individuals as they left the array to determine direction of travel, as well as, to estimate the area where lobsters were located when their eggs hatched.

Environmental Data- A series of Student's t-tests were used to compare distributions of both temperature (^{0}C) and light intensity (lumens/ft^2) between shallow water (14 m) and deep water (37 m).

Results

DAILY PATTERNS OF ACTIVITY:

Acoustic tags were affixed to egg-bearing lobsters in June of 2016 (n=7) and June of 2017 (n=5). Lobsters ranged in size from 78 to 126 mm with a mean of 96.2 ± 5.0. Individuals were detected within the array for an average of 53.4 ± 16.6 days. There was a significant ($P<0.05$) difference in mean activity (m/s^{-2}) between day and night time hours for all 12 tagged lobsters, with all animals expressing a clear nocturnal pattern of behavior, with minimal activity from 06:00 to 19:00 during higher levels of light ($lumen/ft^2$), followed by increased activity from 20:00 to 05:00 during lower levels of light (Fig. 2-2). Peaks in activity were consistent for all monitored animals and occurred just after sunset at either 21:00 or 22:00 hrs. The daily mean distance traveled (km) for all lobsters was 0.39 ± 0.04 km (range: 0.17-0.66).

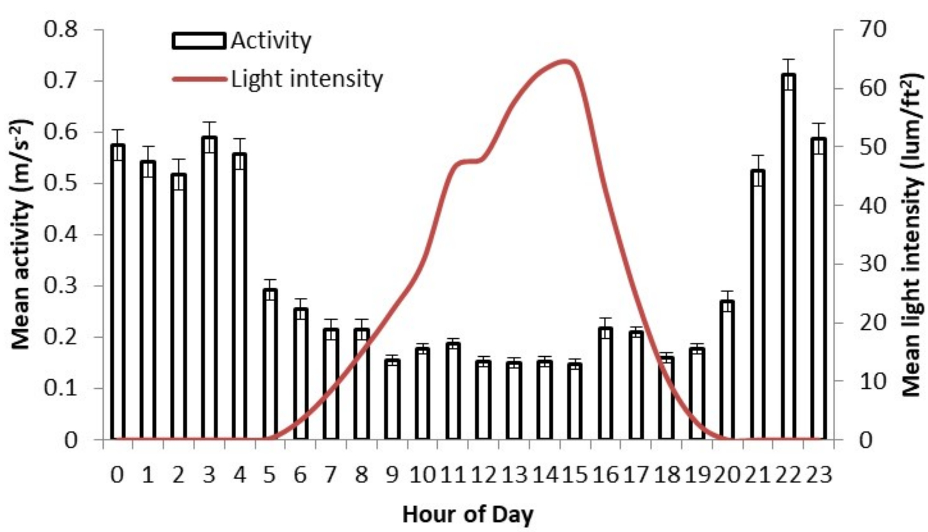

Figure 2-2. The nocturnal pattern of activity expressed by one berried female from 6/17/16-7/4/16. Red line indicates light levels (lumen/ft2) at 14 m. All tagged lobsters showed this same general pattern of increased activity at night. Acceleration values below 0.2 m/s^{-2} are likely indicative of very low levels of activity such as grooming or movement within a shelter, as established by Jury et al. (2018).

DEPTH RELATED MOVEMENTS:

Eleven of the 12 individuals monitored (92%) moved to deeper water (>29 m) prior to the time their eggs were estimated to hatch. The other animal stayed in shallow water at a depth of ~ 15 m. Two basic patterns emerged for the lobsters that moved to deeper water prior to egg hatch: 1) Eight (73%) lobsters stayed in shallow water for a period of time after release and then moved to deep water prior to the time of estimated egg hatch (Fig. 2-3A); and 2) Three lobsters (27%) moved to deeper water less than 24 hrs after they were tagged, then moved back to shallow water before eventually moving deep again prior to the estimated time of hatch (Fig. 2-3B).

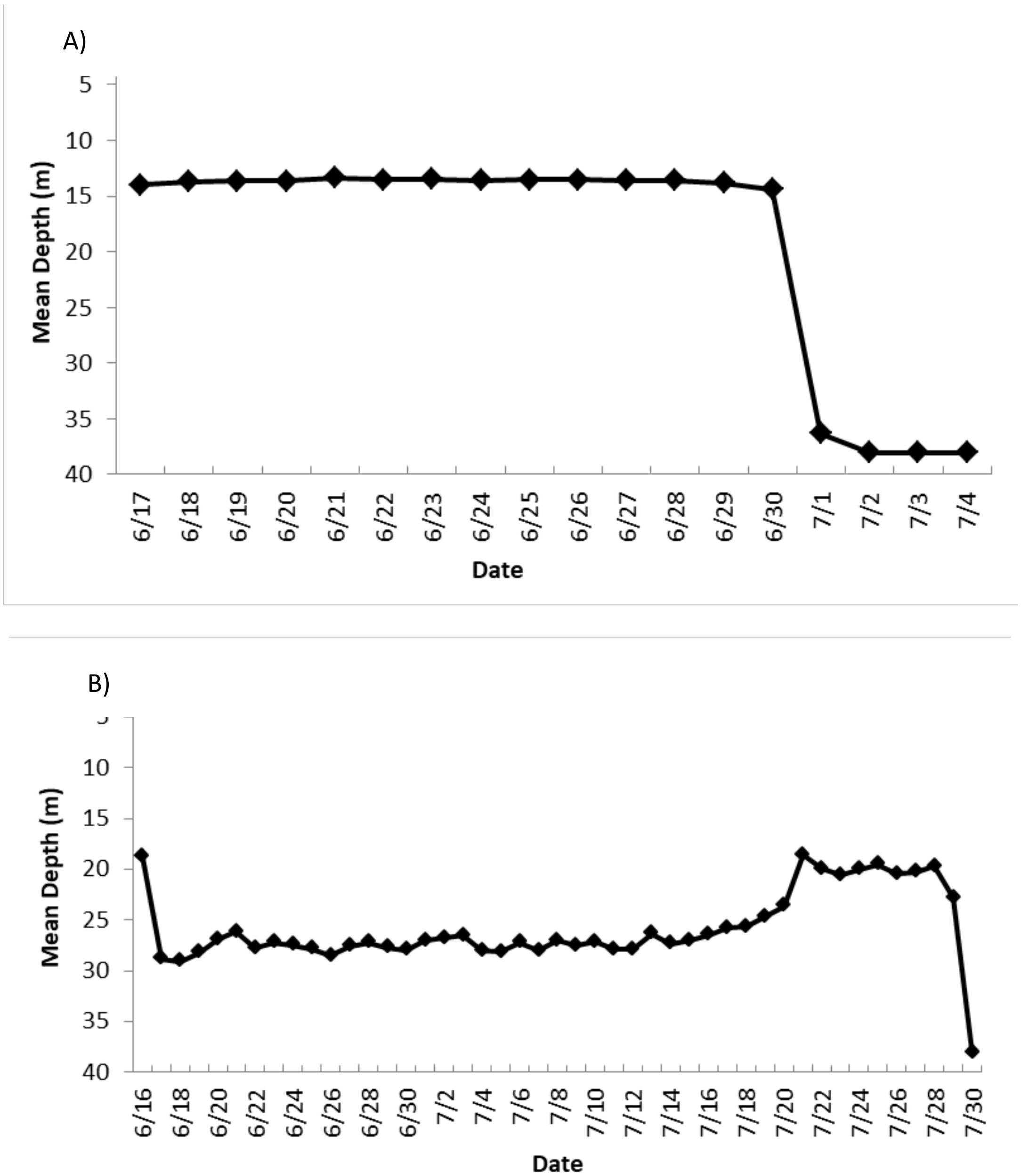

Figure 2-3. (A) Example of a lobster that remained in shallow water for a period of time after tagging, before moving to deep water prior to the time of estimated egg hatch (7/14/16). Standard error for all daily depth estimates <0.1m and (B), depth profile for one of the three lobsters that immediately moved to deep water after being tagged, then back to shallow and then to deep water prior to the estimated time of egg hatch (8/19/2017). Standard error for all daily depth estimates <0.6 m.

All lobsters initiated deep water movements at night between 21:00 and 01:00, and a majority of them (82%) started their migrations just after sunset, between 21:00 and 22:00 (Fig. 2-4). Lobsters displayed a mean descent of 17 ± 1.7 m during deep water movements which took between 1 and 11 days. Lobsters with eggs estimated to hatch within 3 weeks of tagging (n=5), moved to deep water earlier than those with eggs estimated to hatch later in the season (> 3 weeks, n=6).

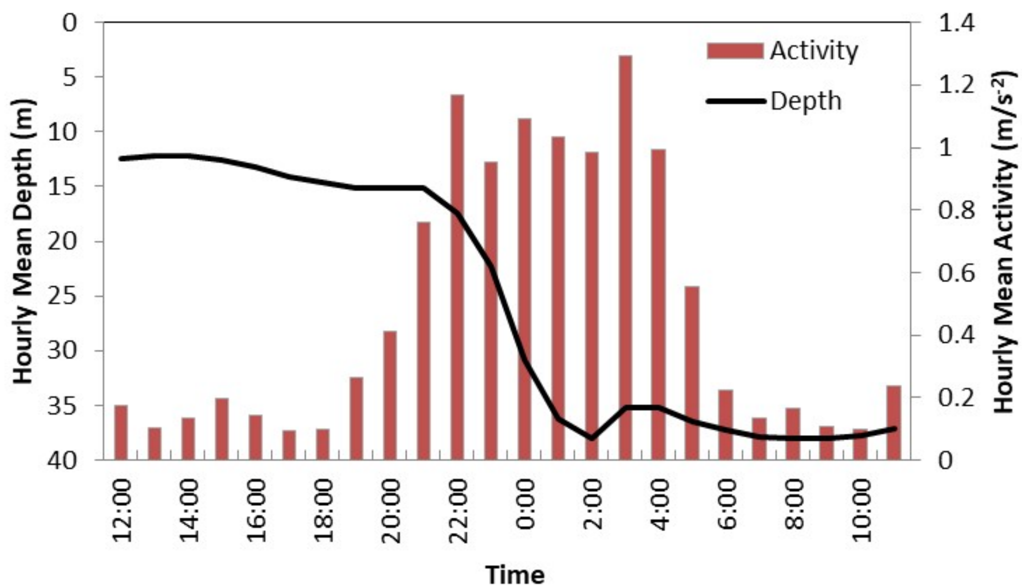

Figure 2-4. The relationship between activity and movement to deep water by one egg-bearing lobster between 6/30-7/1 2017.

HATCHING LOCATIONS:

Eight lobsters (67%) moved to deep water and then continued to towards even deeper water before eventually leaving the array before the time their eggs were estimated to hatch (Fig. 2-5). These lobsters initiated movement to deep water 15.5 ± 2.5 days before estimated hatch, and left the array 12 ± 2.3 days before estimated hatch. A majority of lobsters left the array to the southeast, south or southwest (n=6), and two left in a northeasterly direction. Three lobsters (25%) stayed within the array at depths of 30-40 meters for an average of 4.3 ± 2.3 days during the time we estimated their eggs would hatch before moving out of the array (n=2) or back to shallow water (n=1). Lobsters that hatched eggs within the array continued to exhibit nocturnal activity patterns. These animals initiated their movements to deeper water 7 ± 4.0 days before their estimated hatch time (Fig. 2-6).

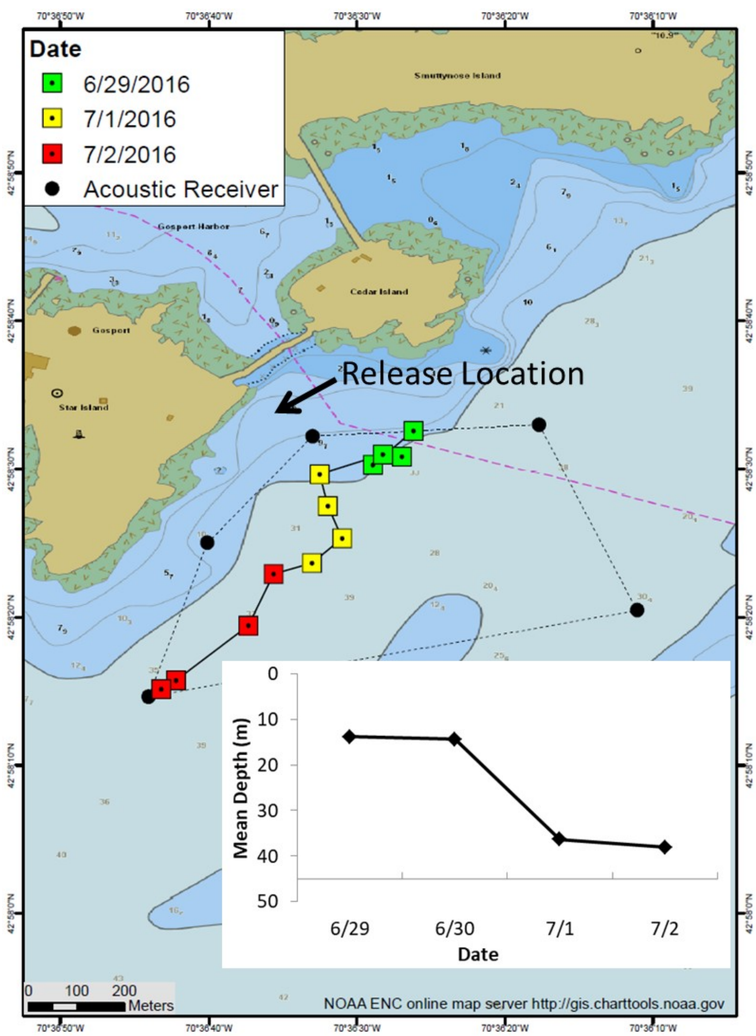

Figure 2-5. The general path and depth profile for a lobster (CL=X, tag date:Y) that moved to deep water and left the array before the estimated time of egg hatch. The majority of these lobsters left in a southeast, south or southwest direction.

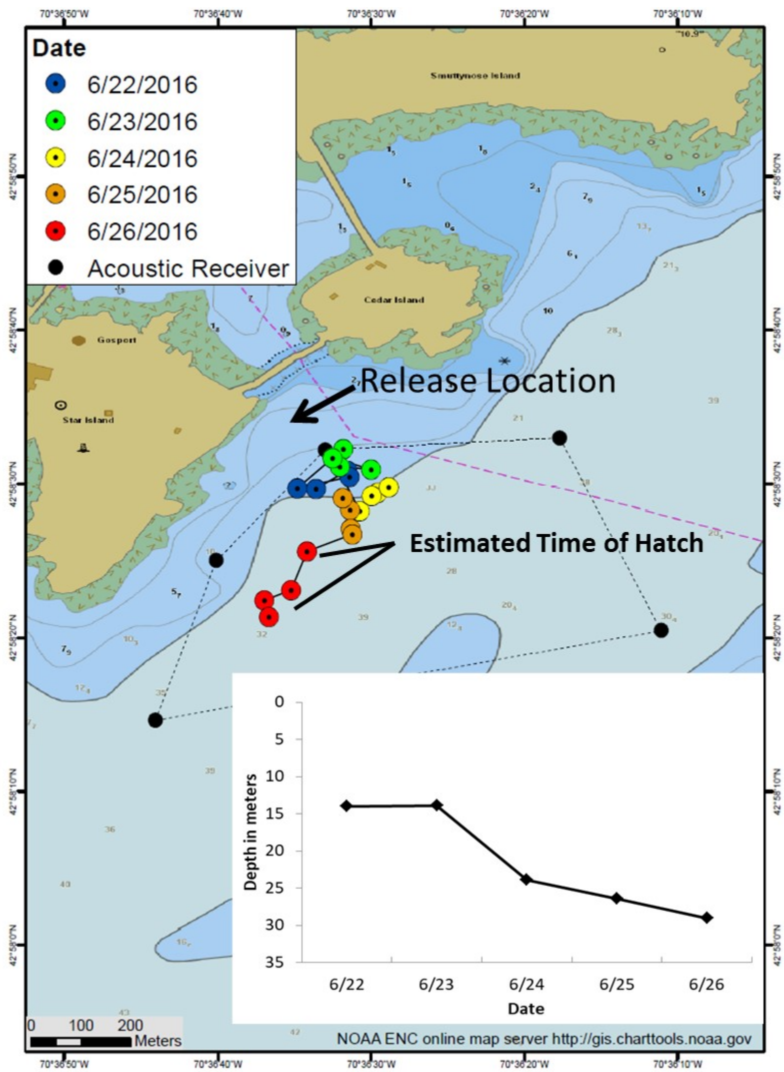

Figure 2-6. The path and depth profile of a lobster that moved to deep water and hatched eggs within the array. All lobsters that displayed deep water movement and stayed within the array were at a depth of 29-40 meters when their eggs hatched.

ENVIRONMENTAL DATA:

Both temperature and light levels varied by depth during the egg brooding and hatching period. There was a significant difference in both water temperature and light intensity between 14 and 37 m ($P<0.05$, unpaired t-test). The mean temperature at 14 m was $11.4 \pm 0.16\ ^0$C, while the mean at 37 m was 7.7 ± 0.12. Mean light intensity (lumens/ft^2) in shallow water was 16.3 ± 1.6, while the mean in deep water was 0.13 ± 0.02. Wave height varied between 0.28 and 1.17 m during the 2016 season and between 0.31 and 1.95 during the 2017 season.

Discussion

The ability to monitor the depth, activity, and spatial movement patterns of egg-bearing lobsters during the late-stage brooding and hatching period has provided new insight into the behavior of this consequential life-stage of the American lobster. In a previous study (Chapter 1; Carloni and Watson, 2018) we found that female lobsters with late-stage eggs were abundant in the shallow waters around the IOS, but those with eggs in the process of hatching were more abundant in deeper water (> 30 m). This led us to conclude that ovigerous lobsters close to hatch were about to hatch moved to deeper water. The telemetry data presented in this Chapter supports that hypothesis. For example, 92% (n=11) of monitored animals displayed movements to deep water prior to the time their eggs were estimated to hatch. Although we don't know the exact location where all of these animals were located when their eggs hatched, the following provide evidence that they were likely in deep water: 1) All but one lobster moved to deep water prior to the estimated time of hatch and those that left the array were moving towards even deeper water, and 2) lobsters with eggs estimated to hatch earlier in the season displayed deep water movement prior to those estimated to hatch later in the season.

Our results, in concert with previous work (Goldstein and Watson 2015, Carloni and Watson 2018) provide strong evidence that American lobster eggs are primarily hatched in deep water in this region. These deep offshore areas are significantly colder, and darker, and the predominant coastal current is stronger (Churchill et al. 2005), and at the present time, it is not clear which of these abiotic factors guide the movements of female lobsters and if they promote the survival and distribution of the larvae. Lab-based studies provide evidence that low light levels and temperatures similar to those observed in deep water around the Isles of Shoals would not hinder survival rates of newly hatched larvae (Templeman 1936, MacKenzie 1988), but they also would not aide in development. Thus, is seems most likely that these offshore areas may provide an ideal location for larval dispersal and survival due to the predominant coastal current.

The Gulf of Maine Coastal Current (GMCC) is centered along the 100 meter isobath and extends to within 10 km of the coast (Churchill et al. 2005). It has been demonstrated that this current affects the transport of larvae; and eggs hatched inside the shoreward edge displayed different trajectories than those hatched within the current (Incze and Naimie 2000, Incze et al. 2010, Goldstein 2012). It may be beneficial for larvae to develop within this current for two reasons. First, there is a more consistent flow that would transport larvae parallel to, rather than towards, the coast (Incze and Naimie 2000, Goldstein Watson 2015). Secondly, there is relatively higher abundance of copepods (*C. finmarchicus*, Runge 2012), a potentially important food source for larval development (Carloni et al. 2018). Offshore deep water movements therefore may be beneficial to the survival and development of larvae to the postlarva stage, however, a majority of postlarvae settle near the coast in warmer water in shallow waters (Wahle et al. 2013). Therefore, the transport dynamics from offshore areas to traditional nursery habitats should also be considered.

In Southern New England, Katz et al. (1994) found a higher abundance of earlier stage larvae in offshore areas (up to 150 km offshore), but more mature larvae closer to shore, suggesting eggs hatched farther offshore recruit to inshore shallow waters. An empirical trajectory model showed that passive drift of these larvae alone was not sufficient for these offshore populations to recruit inshore, however, when incorporating the swimming speed of postlarvae, recruitment to inshore coastal waters was plausible. These results applied to the Gulf of Maine, suggest that with the predominant southwesterly winds and swimming speed of postlava (10-18 cm/s^{-1}), eggs hatched offshore could recruit to known coastal nursery habitats.

There is mounting evidence that American lobsters migrate to deeper offshore areas prior to hatching their eggs, which may be a novel finding for this species, but is a well-known behavior for certain species of spiny lobsters (Peacock 1974, Olsen et al. 1975, Allsopp 1968, Davis 1977, Kanciruk and Herrnkind 1976). It has also been hypothesized that movements of spiny lobster to offshore areas enhances survival of larvae due to favorable offshore conditions where coastal currents/fronts play a large role in the recruitment process due to both their proximity to shore and the availability of food (Phillips and McWilliam 2009). Additionally, ovigerous blue crabs (*Callinectes sapidus*) display directed movements to mouths of estuaries and bays, which allow zoeae to utilize offshore currents and avoid osmotic stress and predators (Forward et al. 2003). Though the life history of American lobster is different from these species, there does appear to be several parallels between the abovementioned studies and results from our work. Additional research on the cues that guide the movements of American lobster, and the spatial distribution of larvae and their potential food sources would increase our understanding of these deep water migrations and their implications on recruitment processes.

Fitting lobsters with accelerometers made it possible to determine when they were most active. While it has been demonstrated that American lobsters are generally nocturnal (Cobb 1969, Ennis 1984, Jury et al. 2005), the only rigorous study of the daily rhythms of lobsters in their natural habitat was carried out by Golet et al. (2006). To our knowledge daily activity patterns for egg-bearing lobsters *in situ* have not been documented, until the present. All lobsters in our study displayed clear nocturnal behavioral patterns, even when they were in deeper, darker, water and even around the time when their eggs were due to hatch. Furthermore, when we used the system developed by Jury et al. (2018) to convert accelerometer data to distance traveled; the results obtained were consistent with previous studies in the laboratory and in the field. In general, lobsters moved between 200-400 meters in a day, with the greatest activity occurring just after sunset.

In summary, a large majority (92%) of egg-bearing lobsters tagged in our study moved to deeper water prior to the time their eggs hatched. Taken together with results from Chapter 1, the Isles of Shoals appears to provide a favorable area for egg-bearing females to aggregate due to the proximity of this location to warm water for egg development and deep offshore water for hatching their eggs. These directed movements likely serve to provide an ideal location for hatching eggs for both survival and dispersal of their larvae. The cues that lobsters are using to guide their movements to these areas are unknown; however, light, temperature, and currents may play an important role. Additionally, it has been shown that Caribbean spiny lobsters may use chemical cues which trigger behaviors that synchronize larval release (Ziegler and Forward 2007), similar cues could be involved in American lobster egg development which could also potentially trigger deep water movements. Research is currently underway to better understand these cues as well as the biological implications of hatching eggs offshore in deep water.

Summary/Future Direction/Management Implications

Below is a summary of the findings from this study, as well as recommendations for future research. Additionally, I discuss the implications this work may have on the management of this species.

Summary of Findings:

- Traps fished on the eastern side of the IOS caught significantly larger female lobsters and ~3 times more egg-bearing lobsters than those on the western side.
- The catch rate of females carrying eggs that were hatching was significantly higher in the deep-water stratum (26-35 m) compared to shallow areas (5-15 m), when combining data from both sides of the IOS. In contrast, late stage pre-hatch animals were significantly more abundant in shallow water.
- Ninety two percent of acoustically monitored lobsters moved to deep water prior to the time their eggs were estimated to hatch. Of these, 25% hatched eggs within the array, while 67% left the array generally in a south southwesterly direction towards deep water.
- Results from Chapters 1 and 2 provide evidence that certain areas around the IOS are more attractive to egg-bearing lobsters and that currents and proximity to deep water may be factors that influence their distribution. The steep bathymetry found on the east side of the IOS may provide the most efficient path for egg-bearing lobsters to access warm water for egg development and deep water for hatching their eggs.
- We hypothesize these movements are undertaken to provide an optimal place for dispersal and survival of larvae.

Future Directions and Implications for Management

This study in combination with past studies from the Watson lab provide evidence that lobsters primarily hatch their eggs in offshore deep water and that these movements may serve to enhance dispersal and survival of larvae. We plan to follow up on this research over the next two years by conducting the following research: 1) Assess the distribution of lobster larvae and their potential food sources at three locations along the coast, offshore (15km), nearshore (7km) and inshore (1km) using a paired neuston net. To our knowledge the spatial distribution of lobster larvae has not been documented in the Gulf of Maine with regards to proximity to shore. If indeed, our hypothesis is correct, a higher abundance of lobster larvae will be captured offshore, which could provide additional evidence of offshore hatch. 2) We will conduct a series of lab studies to determine what cues may be responsible for this directed movement to deep water. For instance, we will set up a temperature controlled experiment to determine if lobsters prefer certain temperatures to hatch their eggs.

This research is important to management for a number of reasons. In Southern New England, research has shown that egg-bearing lobsters moved to cooler deeper water as the temperatures increased. Similar scenarios could be imminent in the Gulf of Maine, and thus, it's important to understand the areas female lobsters prefer to brood and hatch their eggs. Also, the area where eggs are hatched has a direct effect on the dispersal and survival rates of their larvae. It has historically been assumed that females hatch their eggs in the locations where they're found in the spring/early summer with late stage pre-hatch eggs. Our research suggest otherwise, as we've demonstrated that there's a directed movement just prior to hatching their eggs.

An important next step in the progression of this research would be to determine the spatial distribution of females during egg hatch. This is important because if lobsters primarily hatch their eggs offshore, oceanographic bio-physical models would need to account for this, as it could significantly change our knowledge of transport dynamics. Finally, this study, as well as those that have preceded it provide ample evidence that offshore shoals are important to the reproduction of this species and need to be protected from coastal development.

REFERENCES

Aiken, D.E. and S.L. Waddy. 1986. Environmental influence on recruitment of the American lobster, *Homarus americanus*: a perspective. Canadian Journal of Fisheries and Aquatic Sciences. 43: 2258-2270.

Allsopp W. H. L. 1968. Investigations into Marine Fishery Management, Research and Development Policy for Spiny Lobster Fisheries, Report to the Gov. of British Honduras. FAO, Rome.

Davis G.E. 1977. Effects of recreational harvest on a spiny lobster population. Bulletin of Marine Science. 27:223-226

ASMFC. 2006. Stock Assessment Report No. 06-03 (Supplement) of the Atlantic States Marine Fisheries Commission. American Lobster Stock Assessment for PeerReview. ASMFC American Lobster Stock Assessment Subcommittee. 352p.

ASMFC. 2009. Stock Assessment Report No. 09-01 (Supplement) of the Atlantic States Marine Fisheries Commission. American Lobster Stock Assessment for Peer Review. ASMFC American Lobster Stock Assessment Subcommittee. 298p.

ASMFC. 2015. Stock Assessment Report No. 15-01 (Supplement) of the Atlantic States Marine Fisheries Commission. American Lobster Stock Assessment for Peer Review. ASMFC American Lobster Stock Assessment Subcommittee. 438p.

Barshaw D. E. and K. L. Lavalli. 1988. Predation upon postlarval lobsters Homarus americanus by cunners Tautogolabrus adspersus and mud crabs Neopanope sayi on three different substrates: eelgrass, mud and rocks. 48: 119-123.

Bradley S.G. 2003. Timing of aggregation and larval release by Tanner Crabs, Chionoecetes bairdi, in relation to tidal current patterns. Fisheries Research. 65:201-216.

Bertelsen, R.D., and J. Hornbeck. 2009. Using acoustic tagging to determine adult spiny lobster (Panulirusargus) movement patterns in Western Sambo Ecological Reserve (Florida, United States). New Zealand Jour of mar. and freshwater Research. 43: 35-46.

Campbell A. and A.B. Stasko. 1985. Movement of tagged American lobsters, Homarus americanus, off Southwestern Nova Scotia. Can. J. Fish Aquatic. Sci. 42:229-238.

Campbell A. and A.B. Stasko. 1986. Movement of lobsters (Homarus americanus) tagged in the Bay of fundy, Canada. Marine Biology. 92:393-404.

Campbell, A. 1986. Migratory Movements of Ovigerous lobsters, Homarus americanus, tagged off Grand Manan, Eastern Canada. Marine Biology. Vol 92 issues3: 393-404.

Campbell A. and Pezzack, D. S. 1986. Relative egg production and abundance of berried lobsters, *Homarus americanus* in the Bay of Fundy off southwestern Nova Scotia. Can J. Fish. Aquat. Sci. 43: 2190-2196.

Campbell A. 1989. Dispersal of American lobster, Homarus americanus, tagged off Southern Nova Scotia. Canadian Journal of Fisherieis and Aquatic Science. 46(11).

Campbell A. 1990. Aggregations of Berried Lobsters (Homarus americanus) in Shallow Waters off Grand Manan, Eastern Canada. Can. J. Fish. Aquat. Sci., 47: 520-523

Carloni J.T. and W.A. Watson. 2018a. Distibution of ovigerous American lobsters near the Isles of Shoals, New Hampshire. Bull. Mar Sci.

Carloni J.T., Wahle R, Geoghegan P, Bjorkstedt E. 2018b. Bridging the spawner-recruit disconnect: Trends in American lobster recruitment linked to the pelagic food web. Bull Mar Sci. In Press.

Churchill J.H., Pettigrew N.R., Signell R.P. 2005. Structure and variability of the Western Maine Coastal Current. Deep Sea Research. 52:2392-2410.

Crossin, G.T., S. A. Al-Ayoub, S.H. Jury, W.H. Howell, and W.H. Watson III. 1998. Behavioral thermoregulation in the American lobster *Homarus americanus.* Journal of Experimental Biology. 201: 365-374.

Cobb J.S. 1969. Activity, growth and shelter selection of American lobster. PhD thesis. University of Rhode Island, Kingston R.I.

Cooper, R. and J. Uzmann. 1971. Migrations and growth of deep-sea lobsters, *Homarus americanus.* Science. 171: 288-290.

Cowan D.F., Watson W.H. III. Solow A.R. and Mountcastle A.M. 2007. Thermal histories of brooding lobsters, Homarus americanus, in the Gulf of Maine. Mar. Biol. 150:463-470.

Dow, R. L. 1974. American lobsters tagged by Maine commercial fishermen, 1957-59. Fish. Bull. U.S. 72, 622-623.

Dunnington M.J. , R.A. Wahle , M.C. Bell and N.R. Geraldi. 2005: Evaluating local population dynamics of the American lobster, Homarus americanus, with trap-based mark-recapture methods and seabed mapping, New Zealand Journal of Marine and Freshwater Research, 39:6. 1253-1276.

Eagles MD, DE Aiken, SL Waddy. 1986. Influence of light and food on larval American lobsters, *Homarus americanus*. Can. J. Fish. Aquat. Sci. 43: 2303-2310.

Epifanio C.E., C Valenti and A. Pembroke. 1984. Dispersal and recruitment of Blue Crab Larvae in Delaware Bay, U.S.A. Estuarine, Coastal and Shelf Science. 18: 1-12.

Epifanio C. E., K. T. Little and P.M. Rowe. 1988. Dispersal and recruitment of fiddler crab larvae in the Delaware River estuary. Marine Ecology-Progress Series. Vol. 43: 181-188.

Estrella, B.T. and T.D. Morrisey. Seasonal movement of offshore American lobster, Homarus americanus, tagged along the eastern shore of Cape Cod, Massachusetts. Fishery Bulletin. 95:466-476.

Geraldi N.R., R.A. Wahle and M.J. Dunnington. Habitat effects on American lobster (*Homarus americanus*) movement and density: Insights from georeferenced trap arrays

Glenn R.P. and T.L. Pugh. 2007. Random Stratified Ventless Trap Survey Design for Pilot Study in Massachusetts Bay. Agreement Number 05-953

Glenn, B., K. Whitmore, T.L. Pugh, J. Manning, M. Gibson, L. Dellinger, T. Angell, A. DeCosta, R. Wahle and S. Wilcox. 2011. Examining settlement dynamics of postlarval American lobster, (*Homarus americanus*), in Lobster Management Area2.http://static.squarespace.com/static/50529c7ce4b020ebebdf5cfe/t/51798b41e4b0bf1bde32f0cc/1366920001528/CFRF%20B%20%20Glenn%20Settlement%20Final%20Report%20w-appendices.pdf

Goldstein, J.S. 2012. The impact of seasonal movements by ovigerous American lobsters (Homarus americanus) on egg development and larval release. Ph.D. dissertation, University of New Hampshire, Durham, NH.

Goldstein, J.S., and W.H. Watson III. 2015. Seasonal movements of American lobsters in southern Gulf of Maine coastal waters: patterns, environmental triggers, and implications for larval release. Mar. Ecol. Prog. Ser. 524:197-211

Goldstein, J.S., and W.H. Watson III. 2015. Influence of natural inshore and offshore thermal regimes on egg development and time of hatch in American lobsters, *Homarus americanus*. Biol. Bull. 228:1-12

Helluy S.M. and B.S. Beltz. 1991. Embryonic Development of the American lobster (Homarus americanus): Quantitative Staging and Characterization of an Embryonic Molt Cylcle. Biol. Bull. 180:355-377.

Henninger H.P. and J.T. Carloni. 2016. Improving American lobster biological & catch/effort data for Georges Bank, and characterizing American lobster seasonal egger aggregation in Closed Area II (Statisical Areas 561 & 562). Final Report Project # NA15NMF47440253.

Herrick F.H. The American lobster: A study of its habits and development. 1895. Bull. U.S. Fish Comm. 15:1-252

Incze L.S. and Naimie C.E. 2000. Modeling the transport of lobster (*Homarus americanus*) larvae and postlarvae in the Gulf of Maine. Fish. Oceanogr. 9:99-113.

Incze, L, H Xue, N Wolff, D. Xu, C. Wilson, R Steneck, R Wahle, P. Lawton, N Pettigrew, and Y Chenc. 2010. Connectivity of lobster (*Homarus americanus*) populations in the coastal Gulf of Maine: part II. Coupled biophysical dynamics. Fisheries Oceanography 19: 1-20.

Jarvis C. 1989. Movement patterns of late state ovigerous female lobsters (Homarus americanus) Milne-Edwards at Jeddore, Nova Scotia. M.S. thesis. Dalhousie University, Halifax, Nova Scotia, Canada.

Jury, S.H. and W.H. Watson III. 2000. Thermosensitivity of the lobster, *Homarus americanus*, as determined by cardiac assay. Biological Bulletin. 199: 257-264.

Jury S.H. and W.H. Watson III. 2013. Seasonal and sexual differences in the thermal preferences and movements of American lobsters. Can. J. Fish. Aquat. Sci. 70:1650-1665.

Jury S.H., T. Langley, B.C. Gutzler, J.S. Goldstein and W.H. Watson. In Press. Monitoring the behavior of freely moving lobsters with accelerometers. Bull. Mar. Sci.

Kanciruk P. and W.F. Herrnkind. 1978. An indexed bibliography of spiny lobster, family Palinuridae, Fla. Sea Grant Program, Rep. 8:1-101

Katz C.H., J.S. Cobb and M. Spaulding. 1994. Larval behavior, hydrodynamic transport, and potential offshore to inshore recruitment in the American lobster *Homarus americanus.* Marine Ecology Progress Series. 103:265:273

Krouse, J.S. 1980. Summary of lobster, *Homarus americanus*, tagging studies in American waters (1898-1978). Can. Tech. Rep. Fish. Aquat. Sciences 932: 135-140.

Le Bris, A., Mills, K. E., Wahle, R. A., Chen, Y., Alexander, M. A., Allyn, A. J., Shuetz, J. G., et al. 2018. Climate vulnerability and resilience in the most valuable North American fishery. PNAS early access. https://doi.org/10.1073/pnas.1711122115.

McKoy J.L. and Leachman A. 1982. Aggregations of ovigerous female rock lobsters, Jasus edwardsii (Decapoda: Palinuridae). New Zea J. of Marin and Freshwater Reas. 16: 141-146

Mills, K.E. A.J. Pershing, C.j. Brown, Y. Chen. F.S. Chiang. D.S. Holland. S. Lehuta. J.A. Nye. J. C. Sun. A.C. Thomas and R.A. Wahle. 2013. Fisheries Management in a Changing Climate. Oceanography. Download From http://www.tos.org/oceanography.

Morrissey, T.D. 1971. Movements of tagged American lobsters, Homarus americanus liberated 16 off Cape Cod, Massachusetts. Transactions of the American Fisheries Society. 100: 117-120.

Morrissey E.M. 2016. Reproduction and recruitment of American Lobster (*Homarus americanus*) in the Great Bay Estuary, New Hampshire. Thesis, University of New Hampshire, Durham, NH.

Nicol S., 2006. Krill, Currents, and Sea Ice: Euphausia superba and its Changing Environment. BioScience. Vol.56 No. 2.

NOAA 2015. Fisheries of the United States. Current fishery statistics No. 2016

NOAA 2017. NOAA Office of Science and Technology. Commercial Fisheries Statistics. Website:http://www.st.nmfs.noaa.gov/commercial-fisheries/commercial-landings/annual-landings/index_Acccesed 8/12/2017.

NHF&G 2014. Programs improving management of ASMFC managed species in New Hampshire, Lobster Sea Sampling annual report. Job 1.

NHF&G 2015. Programs improving management of ASMFC managed species in New Hampshire, Final Report NA10NMF4740359, Lobster Sea Sampling. Job 1

Olsen D. W.F. Herrinkind and R. Cooper. 1975. Population dynamics, ecology and behavior of spiny lobster, *Panulirus argus*, of St. John. U.S. Virgin Islands: Introduction Sci. Bull. Nt. Hist. Mus. Los Angeles Cty, 20:11-16

Pandian, T. J. 1970. Yolk utilization and hatching in the Canadian lobster *Homarus americanu*s. Mar. Biol. 7: 249-254

Peacock N.A. 1974. A study of spiny lobster fishery of Antigua and Barbuda. Gulf of Caribb. Fish Inst., University of Miami, Proc. 26:117-130.

Perkins, H. 1972. Developmental rates at various temperatures of embryos of the northern lobster (Homarus americanus Milne Edwards). Fish Bull. 70: 95-99

Phillips B.F. and P.S. McWilliam. 2009. Spiny lobster development: where does successful metamorphosis to puerulus occur? a review. Rev. Fish Biol Fisheries. 19:193-2015.

Robichaud, D.A. and A. Campbell. 1991. Annual and Seasonal Size Frequency Changes of Trap-caught Lobsters (Homarus americanus) in Bay of Fundy. J. Northw. Atl. Fish. Sci. 11:29-37.

Runge J.A., Jones R.J., Record N.R., Pershing A.J. 2012. Summer distribution of the planktonic copepod, Calanus finmarchicus, along the coast of Gulf of Maine. Report for the State of Maine's Department of Marine Resources.

Runge J.A., Rubao J.I., Thompson C.R.S., Record N.R., Chen C., Vandemark D.C., Salisbury J.E., Maps F. 2015. Persistence of Calanus finmarchicus in the western Gulf of Maine during recent warming. Journal of Plankton Research. 37:221-232

Saila S.B. and J. M. Flowers. Movement and Behavior of Berried Female Lobsters Displaced from Offshore Areas to Narragansett Bay, Rhode Island. ICES Jour. Of Mar. Sci. 31: 342-351.

Simpfendorfer C.A., M.R. Heupel and R.E. Hueter. 2002. Estimation of short-term centers of activity from an array of omnidirectional hydrophones and its use in studying animal movements. Can. J. fish. Aquat. Sci. 59:23-32

Steneck R. 2000. Lobster tagging: How far, how deep and how fast? Report to the Maine Department of Marine Resources.

Stone P.P. and C.E. O'Clair. 2002. Behavior of female Dungeness crabs, Cancer magister, in a glacial southeast Alaska estuary: homing, brooding-site fidelity, seasonal movements and habitat use. J. Crustac Biol 22:481-492

Talbot P and S. Helluy. 1995. Reporoduction and embryonic development. In: Factor JR (ed) Biology of the lobster *Homarus Americus.* Academic Press, San Diego, CA, p 177-2016.

Tankersley, R. A., M. Wieber, M. Sigala, and K. Kachurak. 1998. Migratory Behavior of Ovigerous Blue Crabs *Callinectes sapidus*: Evidence for Selective Tidal-Stream Transport. Biol. Bull. 195: 168-173

Templeman, W. 1940. Embryonic development rates and egg laying of Canadian lobsters. J. Fish Res. Board Can. 5: 71-83

Uzmann J. R., R.A. Cooper and K.J. Pecci. 1977. Migration and Dispersion of Tagged American Lobsters, Homarus americanus, on the Southern New England Continental Shelf. NOAA Technical Report NMFS SSRF-705.

Waddy, S.L., and D.E. Aiken. 1995. Temperature regulation of reprocuction in female American lobsters (Homarus americanus). ICES Symposium on Fisheries and Plankton Acoustics, July 12-15, 1995, Aberdeen, Scotland. Mar. Sci. Symp. 199: 54-60

Wahle, R.A. & Steneck, R.S., 1991. Recruitment habitats and nursery grounds of the American lobster *Homarus americanus*: a demographic bottleneck? *Marine Ecology Progress Series*, 69, pp. 231-243.

Wahle, R.A. & Steneck, R.S., 1992. Habitat restirictions in early benthic life: experiments on habitat selectin and in situ predation with the American lobster. J. Exp. Mar. Biol. Ecol. 157: 91-114

Wahle, R.A. & Incze, L.S., 1997. Pre- and post-settlement processes in recruitment of the American lobster. *Journal of Experimental Marine Biology and Ecology*, 217 (1997), pp. 179-207.

Wahle, R.A., C.Bergeron, J. Tremblay, C. Wilson, V. Burdettt-Coutts, M. Comeau, R. Rochetete et al. 2013. Marine Biology Research. 1:42-58

Watson, W.H., A. Vetrovs and W.H. Howell, 1999. Lobster movements in as estuary. MarineBiology 134: 65-75.

Watson, WH III, JS Goldstein, EM Morrissey, HA Cole and TL Pugh. 2017. Evidence of mating by sexually immature female American lobsters *Homarus americanus* (H. Milne Edwards, 1837) (Decapoda: Nephropidae). 2017. J. Crustacean Biol. 37(1): 2-6.

Ziegler T.A. and R.B. Forward. 2007. Control of larval release in the Caribbean spiny lobster, *Panulirus argus*: role of chemical cues. Marine Biology.